FEEDING HABITS OF THE YELLOWTAIL FLOUNDER and PRODUCTION OF ITS INVERTEBRATE PREY on GEORGES BANK

by

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Signature of Author . . . . . .
Massachusetts Institute of Technology/
Woods Hole Oceanographic Institution
9 August 1985

Certified by . . . . . .
J. Frederick Grassle, Thesis Supervisor

Accepted by . . . . . .
John J. Stegeman, Chairman
Joint Committee for Biological Oceanography,
Massachusetts Institute of Technology/
Woods Hole Oceanographic Institution

In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of inanimate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten", but in order to understand the higher intricasies of any ecological system, it is most easy to start from this crudely simple point of view.

G. Evelyn Hutchinson, 1959
Homage to Santa Rosalia or
Why are there so many kinds of animals?
American Naturalist 93: 145-159

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ABSTRACT

As part of the Georges Bank Benthic Infauna Monitoring Program, size-frequency analysis was used to study the life history and production of three benthic amphipod species: Ampelisca agassizi, Unciola inermis and Ericthonius fasciatus. Abundant over large areas of Georges Bank, these amphipods are important prey of yellowtail flounder. From benthic grab samples collected quarterly during 1981 to 1983, over 200 individuals of each species were measured for each sampling date. The computer program NORMSEP separated the length-frequency distributions into cohorts. Growth and mortality rates were determined by following cohorts through time; production was calculated as the sum of growth increments. Differences in the population dynamics of the three species were exemplified by annual production-to-biomass ratios (P/B). E. fasciatus had the highest P/B (2.8 to 4.1), followed by U. inermis (1.3 to 2.7) and A. agassizi (1.3 to 1.4). These results, the first direct production estimates for benthic macrofaunal species on Georges Bank, are compared to production estimates for other marine amphipod species. Amphipod production rates on Georges Bank are as high as production rates of related near-shore species with similar life-spans.

The Northeast Fisheries Center sampled yellowtail flounder stomachs at three sites on four quarterly dates from August 1982 to May 1983. As closely as possible, stomach sampling coincided with the dates and locations of benthic monitoring to enable direct comparison between ingested and available food. Stomach contents were sorted and weighed and important prey species were measured. Yellowtail flounder feed mainly on benthic macrofauna; amphipods and polychaetes are the most important prey groups. Although the diet composition varied among stations and dates, in each case a few prey species constituted the bulk of the diet. Selection indices were calculated to compare the species composition of the stomach contents to that of the benthic macrofauna. Food selection by yellowtail flounder is explained on the basis of prey life history and prey size. The species- and size-selection indices account for most of the variability in diet composition. A log-normal curve was fit, by least squares, to the size-selection indices; according to this fit, the optimum prey weight for yellowtail flounder is 21 mg.

The rate of food consumption by yellowtail flounder was calculated by two methods. The bioenergetic method sums the food required to satisfy the energetic requirements of the fish. The second method is based on the weight of stomach contents and the rate of food evacuation from the stomach. The bioenergetic method gave consistently higher results (1.4 to 1.6 kg fish^{-1} yr^{-1}) than the stomach-content method (0.5 to 0.8 kg fish^{-1} yr^{-1}). Yellowtail flounder abundance was estimated by a method that uses the commercial catch data to standardize the survey, relative-abundance index. These abundance estimates were divided by the appropriate areas to obtain yellowtail flounder density estimates for fall 1982 of 20.0 and 41.3 fish per hectare for Georges Bank and Southern New England, respectively. Consumption rates per fish were multiplied by flounder density to obtain estimates of consumption per unit area, which range from 1.2 to 6.3 gww m^{-2} yr^{-1}. Annual production of six important prey species was calculated. Yellowtail flounder consumption as a percentage of prey production was 6 to 12%, 2 to 5%, and 1 to 3%, for the amphipods Unciola inermis, Ericthonius fasciatus and Ampelisca agassizi, respectively; 11 to 34% and 7 to 21% for the polychaetes Chone infundibuliformis and Nephtys incisa, respectively; and less than 1% for the sand dollar, Echinarachnius parma.

Thesis Supervisor: Dr. J. Frederick Grassle, Senior Scientist,
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Special thanks are due to Dr. M.D. Grosslein of the Northeast Fisheries Center, Woods Hole, for coordinating the fish-stomach sampling. Ray Bowman and Bill Michaels helped collect the stomachs. I thank Dr. N. Maciolek-Blake of Battelle New England Marine Research Laboratory for her support in making samples and data available to me. I thank Debbie McGrath, Ellie Baptiste and all the other people at Battelle who sorted and identified samples.

To all the benthons in Redfield basement I am grateful: to Linda Morse-Porteous, Brian Dade and Howard Sanders for insightful discussions, to Susan Brown-Leger who taught me how to tell the girls from the boys (amphipods) and to Rose Petrecca who organized the benthic sampling. Carla Curran analyzed the sand dollar samples as a Summer Fellow and analyzed the Station 5-28 amphipods as a Research Assistant in the fall of 1984; I thank her for her enthusiastic help.

Peggy Dimmock typed the appendices. Figures 1-3 through 1-6, 1-8 and 1-9 are herein reproduced from Collie (1985) with permission of the publisher, Inter-research. Figures 3-3 and 3-4 are redrawn from Collie and Sissenwine (1983).

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PREFACE

Continental shelves constitute only 10% of the ocean floor, yet over half the world catch of marine fish is produced in shelf waters. The high productivity of continental shelves is attributable to their shallow depths, which concentrate fish for economic harvesting and allow greater nutrient recycling with the overlying water column (Walsh 1981). The importance to humans of the continental shelves is underscored by recent oil and gas exploration and the declaration of 200 nautical mile exclusive economic zones by many coastal nations (see Oceanus 27(4)). Oceanographic research on continental shelves is complicated by the great distances involved and the need for ocean-going ships. Direct experimentation is difficult because any instrument strong enough to withstand the currents and waves is likely to introduce experimental artifacts.

Georges Bank is part of the continental shelf off the eastern coast of North America. The waters over this shallow submarine plateau are known to support high production rates of phytoplankton and fish (Backus, in press, Chpts. 21 and 31). However, the energy pathways between phytoplankton and fish are not well understood. The Georges Bank energy budget (Sissenwine et al. 1982) provides a useful framework for studying the food web and points out gaps in our measurements of standing stocks and flux rates. In particular, little is known about the coupling of pelagic and benthic processes: how the energy from primary production is transformed into the benthic invertebrates that, in turn, are food for many species of demersal fish.

Walsh (1981) presented a preliminary carbon budget for the northeastern continental shelf from Georges Bank to Cape Hatteras. Of

the total primary production at mid-shelf (about 340 gC m^{-2} yr^{-1}), a large proportion apparently transfers to the sea bottom as phytodetritus (200 gC m^{-2} yr^{-1}) and fecal pellets (40 gC m^{-2} yr^{-1}). Utilization of organic carbon by benthic infauna, as estimated from benthic respiration and production, accounts for about 50 gC m^{-2} yr^{-1}. The remaining 190 gC m^{-2} yr^{-1} lost from the water column is either buried or exported, or it must be utilized by organisms not considered in the carbon budget (e.g. microbial respiration). Walsh probably overestimated primary production by about 50% (G.T. Rowe, personal communication), but even so, benthic respiration would only account for one third of the carbon reaching the bottom.

This thesis concentrates on one segment of the Georges Bank food web: production of benthic invertebrates and predation on these invertebrates by the yellowtail flounder. I approached this topic from a number of perspectives: as a study of amphipod population dynamics, a study of food selection by yellowtail flounder, a quantification of part of the Georges Bank food web, and finally as a study of the interaction between predator and prey populations. In this thesis I address the following questions: What are the rates of amphipod production? On what basis do yellowtail flounder choose their prey? How do flounder respond to changes in abundance of their preferred prey? What is the rate of food consumption by yellowtail flounder? Does the rate of prey production limit flounder feeding? Conversely, is fish predation a significant source of mortality to the prey populations?

CHAPTER ONE

AMPHIPOD LIFE HISTORY AND PRODUCTION

INTRODUCTION

The earliest reported benthic samples from Georges Bank were the dredge collections made by Smith and Harger (1874). More recently, between 1957 and 1964, the Benthic Dynamics Group of the Northeast Fisheries Center conducted an extensive benthic survey of the U.S. east coast (Wigley 1968). On Georges Bank, samples were collected from more than 150 evenly-distributed stations. Dickinson and Wigley (1981) analyzed the amphipods from these samples and documented the distribution of gammaridean amphipods on Georges Bank. These early studies established the taxonomy and distribution of benthic species; little information concerning life history was obtained.

In 1977 the New England Outer Continental Shelf Benchmark Program was conducted to obtain baseline data on benthic community structure prior to exploratory oil and gas drilling. Forty-two stations on Georges Bank and adjacent areas were sampled quarterly. Data from all four seasons are available from only 11 of these stations (Michael et al. 1983). This report described the faunal composition of these sites over one year, but did not provide any information on the life histories of dominant species. Nine of the 11 Benchmark stations were later adopted in the Georges Bank Benthic Infauna Monitoring Program (GBMP).

During a two-year period, from May 1980 to July 1982, benthic samples were collected at three sites in conjunction with U.S. Geological Survey studies of sediment transport dynamics; two of these sites were adopted as regional stations in the GBMP. Together, the USGS and GBMP

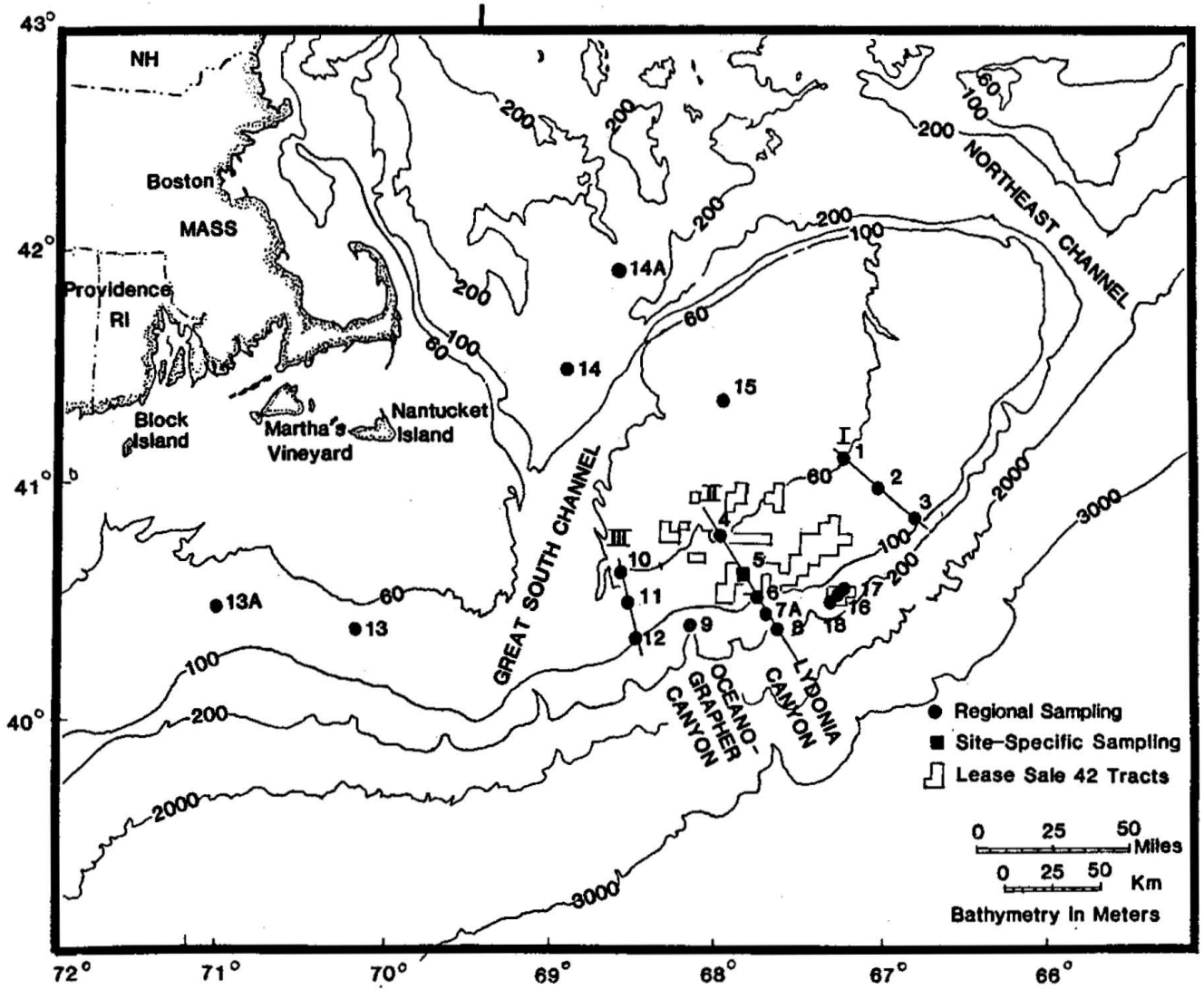


Figure 1-1. Locations of stations sampled by the Georges Bank Benthic Infauna Monitoring Program.

samples provide a four-year time series of benthic species abundance on Georges Bank.

The Georges Bank Benthic Infauna Monitoring Program (GBMP) was designed to trace discharges from oil and gas exploration and to determine their effects on benthic species and communities (Battelle and WHOI 1985). Quarterly sampling was conducted from July 1981 to June 1984. On each date, 18 regional (Fig. 1-1) and 29 site-specific stations were sampled. The site-specific stations were located in an array centered at Regional Station 5 (Fig. 1-2). Repeated sampling during the GBMP provided an opportunity to study the life history of dominant benthic species on Georges Bank.

Steimle (in press) used the biomass data from the 1957-to-1964 and 1977 benthic surveys to estimate macrofaunal production on Georges Bank. He estimated production by partitioning the biomass data among the major taxa and applying a representative production-to-biomass ratio (P/B) to each taxon. The amphipod production estimates I present in this chapter are the first direct estimates of macrofaunal production on Georges Bank. Many, but not all, of the results in this chapter have been presented in Collie (1985) and in Collie and Curran (1985); this chapter includes additional amphipod life-history data.

In this chapter I am concerned with the life histories and production rates of three benthic, gammaridean amphipod species: Ampelisca agassizi Judd (Ampeliscidae), Unciola inermis Shoemaker (Aoridae) and Ericthonius fasciatus Stimson (Ischyroceridae). All three species are tubicolous, subtidal and widely distributed (Bousfield 1973), but little is known about their life cycles. The species called Ericthonius fasciatus in this thesis has been called E. rubricornis by Bousfield (1973) and other authors. However, the genus Ericthonius was

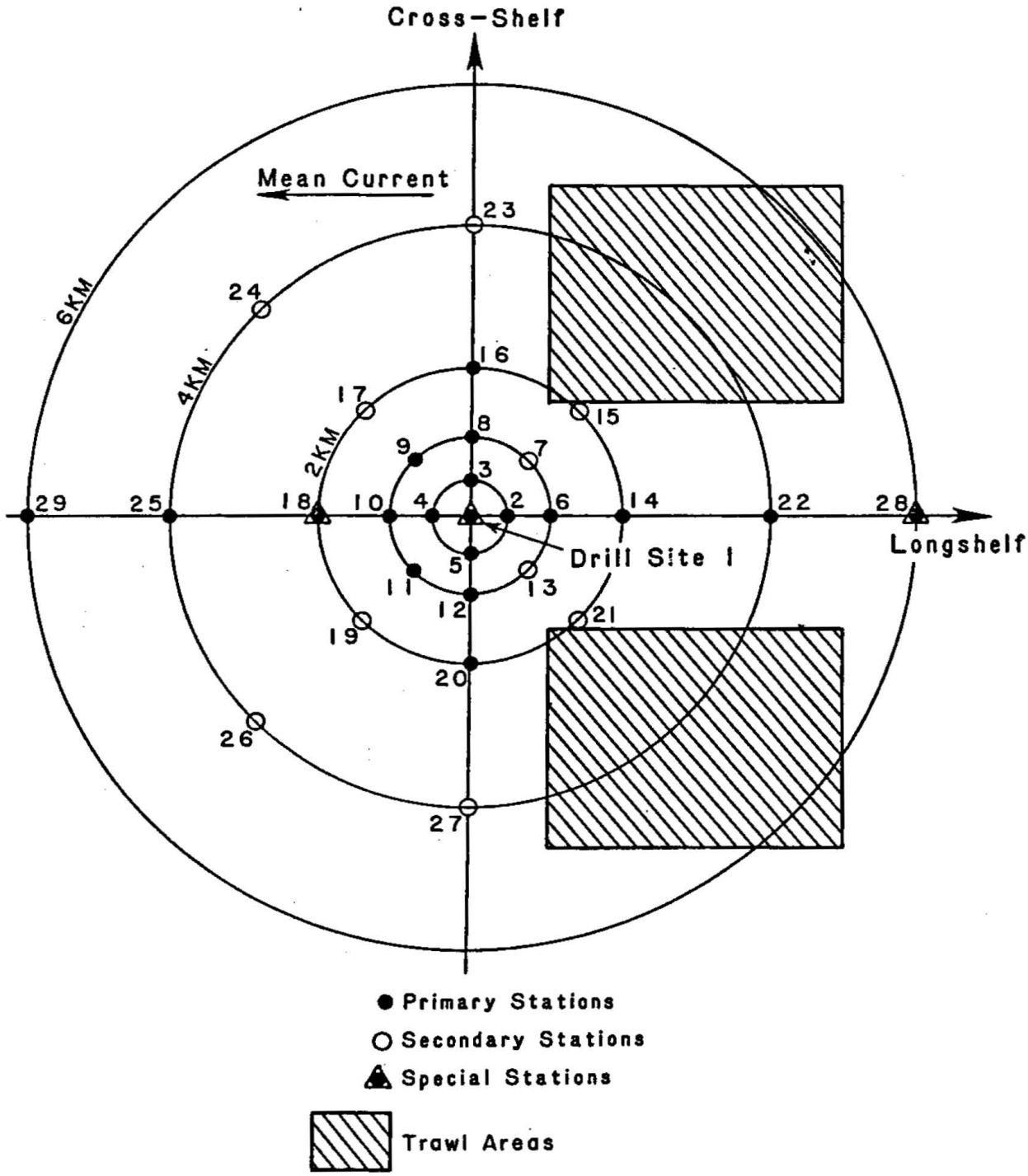


Figure 1-2. Site-specific stations and fish-trawling areas centered at Regional Station 5.

recently revised by Myers and McGrath (1984), and since the Ericthonius I studied fit the description of E. fasciatus by Myers and McGrath, the more recent appellation will be followed.

Ampelisca agassizi lives along both American coasts; in the northwestern Atlantic it has been collected from Nova Scotia to the Caribbean at depths of 5 to 450 m (Mills 1967a). On Georges Bank, A. agassizi has been found in high densities between 60 and 170 m (Dickinson and Wigley 1981). Unciola inermis is distributed along the North American Atlantic coast from Labrador to North Carolina at depths of 0 to 200 m (Shoemaker 1945). U. inermis inhabits the perimeter of Georges Bank between 57 and 192 m (Dickinson and Wigley 1981). Ericthonius fasciatus has an amphi-Atlantic distribution; along the North American coast it has been collected from Labrador to Cape Hatteras at depths of 0 to 400 m (Dickinson et al. 1980). E. fasciatus inhabits the perimeter of Georges Bank between 40 and 192 m (Dickinson and Wigley 1981).

In benthic samples collected during the three-year course of the GBMP, Ampelisca agassizi was found to be the most numerous macrofaunal species when a grand sum was taken of the species counts in all replicates, from all regional stations, from all sampling dates. Ericthonius fasciatus was fourth and Unciola inermis was the 21st most numerous out of 959 enumerated species. All three amphipod species were found in large numbers in the stomachs of several demersal fish species collected off the U.S. east coast by Bowman and Michaels (1984).

These amphipods are good candidates for study because their recruitment is synchronous, which allows cohorts to be identified in the length-frequency distributions. Because female amphipods brood their young, there are no pelagic larvae and all life stages can be collected by benthic samplers. Amphipods don't produce growth rings; therefore I

used size as a surrogate measure of age. The method I use to estimate production depends on being able to identify cohorts and to follow the fate of these cohorts through time.

Four commonly used methods of computing cohort production are increment summation, removal summation, instantaneous growth and the Allen curve. Each of these may be used either in instantaneous, exponential form or in discrete, linear form. The instantaneous form applies when growth and mortality rates are constant and biomass changes exponentially. Gillespie and Benke (1979) showed that under these conditions, the four methods are exactly equivalent. In discrete, linear form, the increment-summation and removal-summation methods are exactly equivalent, but the instantaneous-growth and Allen-curve methods merely appoximate the first two.

Jensen (1919) first proposed a rationale for cohort-based production estimates. Sanders (1956) modified Jensen's inaccurate method into what is known now as the removal-summation method. A good explanation of how the increment-summation and removal-summation methods are applied to field data is given by Crisp (1984).

MATERIALS AND METHODS

This analysis is based on samples collected quarterly during the first two years of the GBMP (July 1981 to July 1983). At each station, on each sampling date, six replicate, 0.04-m^2, modified van Veen grab samples were collected, sieved, and preserved. All replicates were taken within 100 m of the station coordinates. Workers at Battelle Marine Research Laboratory resieved each sample on a 0.3-mm screen, then sorted, enumerated and identified to species the organisms recovered. Size selectivity should not be a problem here because a 0.3-mm sieve retains all life stages including dislodged eggs.

I chose Regional Stations 5 and 13 for this study because fish stomachs also were collected at these sites. Station 5 at 84 m depth is characterized by medium-to-coarse sand. At this site, Unciola inermis and Ericthonius fasciatus are among the five most numerous macrofaunal species. Samples of these two species were analyzed from Site-specific Station 5-1 (July 1981 to July 1983) and from Site-specific Station 5-28 (July 1982 to July 1983). The samples from Station 5-28 were analyzed to compare production of the same species at two adjacent sites (see Fig. 1-2 for site-specific station locations). I analyzed Ampelisca agassizi from Station 13, where it is, numerically, one of the top five species. The sediments at Station 13, located at 69 m in the area south of Nantucket known locally as "the mudpatch", are predominantly very fine sand, silt and clay. The sediments and fauna at these sites are described more completely in Battelle and WHOI (1985).

I measured the amphipods with a digitizer coupled to a microcomputer. (Carla Curran analyzed the Station 5-28 samples.) Each animal was measured from the tip of its rostrum to the base of its telson

(Bousfield 1973; see arrows in Fig. 1-10) by tracing a camera lucida projection with the digitizer wand. An internal calibration factor allowed immediate conversion from digitizer units to length in millimeters. Sample sizes permitting, at least 200 amphipods of each species from each sampling date were measured. Replicates were digitized until the replicate containing the 200^{th} animal was completed, or until all replicates were measured, whichever came first. For cases in which not all replicates were measured, each frequency was scaled to determine the expected number of amphipods of that size, had every individual been measured.

In addition to length, I measured a number of life-history parameters. For most of the samples, I classified adult (larger than 5 mm) amphipods by sex. I used the G-test to test the sex ratios against a 1:1 ratio and against the sex ratio of amphipods found in yellowtail flounder stomachs (see Chapter 2 for details of fish-stomach analysis). The eggs of these amphipod species develop and hatch in the marsupium formed by the females oostegites (brood plates). I further classified adult females into three categories: ovigerous females, females with setose oostegites, and females with developing oostegites. Number of embryos in the brood pouch was recorded for each ovigerous female. Using microscissors, I dissected a number of females to ascertain the state of ovary development. Parasites were sketched and their occurrence recorded.

I used modal analysis to identify cohorts in the length-frequency data. The computer program NORMSEP, written in FORTRAN by Tomlinson (1971) using Hasselblad's (1966) algorithm, separates length-frequency sampling distributions into component normal distributions. In essence, this is a computer-equivalent of the probability-paper method (Harding 1949). NORMSEP uses a maximum-likelihood function to minimize the

difference between observed and expected frequency distributions, and a chi-square statistic measures the goodness of fit. NORMSEP calculates mean length, standard deviation, and number of individuals in each component distribution.

Owing to the minimum number of measurements required for a length-frequency distribution, and the maximum number of amphipods it was practical to measure from each sample, I was unable to generate replicate length-frequency distributions. I assumed, therefore, that a sample size of 200 represented the true size distribution of the entire population. To test the validity of this assumption, I performed a bootstrap analysis of the Unciola inermis size-frequency data from July 1981 at Station 5-1. The bootstrap is used to indicate the sensitivity of my method of size-frequency analysis to sampling variability.

By sampling with replacement from the observed distribution, I produced 20 sets of simulated length-frequency data. The FORTRAN function RAN generates psuedo-random decimals that are uniformly distributed from 0 to 1. To get seed numbers for the different trials I took the first 20 extensions from the WHOI telephone directory, written in reverse order as negative decimals. This ensured a different sequence of random numbers in each trial.

The number of random numbers generated in each trial (249) equalled the number of length measurements made on that sample. The observed length-frequency data were transformed to a cumulative frequency distribution from 0 to 1. This distribution was used to place each random number in the appropriate length class. In this manner, I simulated 20 sets of length-frequency data, each similar to the observed distribution but differing by random variation. I applied the program NORMSEP to each length-frequency distribution in turn to estimate the

parameters of the component modes; the means, variances and covariances of these bootstrap parameter estimates were calculated.

To eliminate potential preservation bias, I determined length-weight relationships for each species using live animals collected in May 1983. To obtain live weights, I damp dried individual animals and weighed each to 0.01 mg on a Mettler balance. Then after anaesthetizing with FINQUEL, I measured each animal with the digitizer. To describe the relationship between length (L) and weight (w) I fit, for each species, by linear regression, a line of the form,

$$\log(w) = a + b\log(L) \ . \qquad (1.1)$$

For groups of animals, each group with a total fresh weight of between 20 and 30 mg, I ascertained ash-free dry weight by drying the samples to constant weight at 60°C and combusting at 450°C for 5 hours.

To determine growth and mortality rates , I followed the mean length and numbers of each cohort through time. I converted mean length of the animals in a cohort to mean weight using the length-weight regressions. Equation 1.1 applies for individual animals but not for the mean of a length distribution. Because weight is a power function of length, the weight corresponding to the observed mean length underestimates the true mean weight by an amount dependent on the variance of length. Pienaar and Ricker (1968) provided formulae that approximate the true mean weight given that the length-weight relationship (Eq. 1.1) and variance of length (s^2) are known. For the case in which 1 b 3:

$$\bar{w} = a(L^b + cL^{b-2}s^2) \qquad (1.2)$$

The values of a and b are as fitted to Eq. 1.1; the value of c, which depends on b, can be found in Table II of Pienaar and Ricker (1968).

I used the increment-summation method described by Crisp (1984) to calculate annual production. Production (P) of each cohort is the sum of weight increments over time (t) according to:

$$P = \sum_{t} \frac{N(t) + N(t+1)}{2} (\bar{w}(t+1) - \bar{w}(t)) \qquad (1.3)$$

where N(t) and $\bar{w}(t)$ are, respectively, the number and mean weight of individuals in the cohort at time t. Annual production of a given species is the sum of each cohort's production over one year.

RESULTS

Observed length-frequency distributions are plotted in Figs. 1-3, 1-4, and 1-5. The frequencies are based on six replicate 0.04-m^2 grab samples, giving a total area of 0.24 m^2. White blocks in the histograms represent ovigerous females. The mean size of juveniles still in the marsupium was 1.8 mm for Ampelisca agassizi and 1.4 mm for both Unciola inermis and Ericthonius fasciatus; therefore peaks in the length-frequency distributions at these lengths correspond to newly released juveniles. Cohorts are named according to the year (and season) in which they were released.

Ampelisca agassizi at Station 13 (Fig. 1-3) appears to be a biennial species in that females of a given generation breed at age 1 and at least some survive to breed at age 2. For example cohorts 80A and 80B had ovigerous females in November 1981 and again in July 1982, while cohort 81B had ovigerous females in November 1982 and again in May 1983. The timing of reproduction varied from year to year. In 1981 ovigerous females were found only in November and recruitment of juveniles occurred in the late fall. Recruitment was delayed in 1981 because cohort 79 did not survive to breed for a second year. In 1982 the breeding season was advanced with ovigerous females present in July and November and recruitment in the late summer. The breeding season was even more advanced in 1983 with ovigerous females present in May and July. Recruitment of juveniles had not occurred by July suggesting that either juveniles were released and lost from the sampling area or the development time of embryos is longer than 2 months. The minimum and maximum lengths of ovigerous females were 5.4 and 10.1 mm, respectively. A length of 10 mm may be reached after the maximum life-span of 2 years.

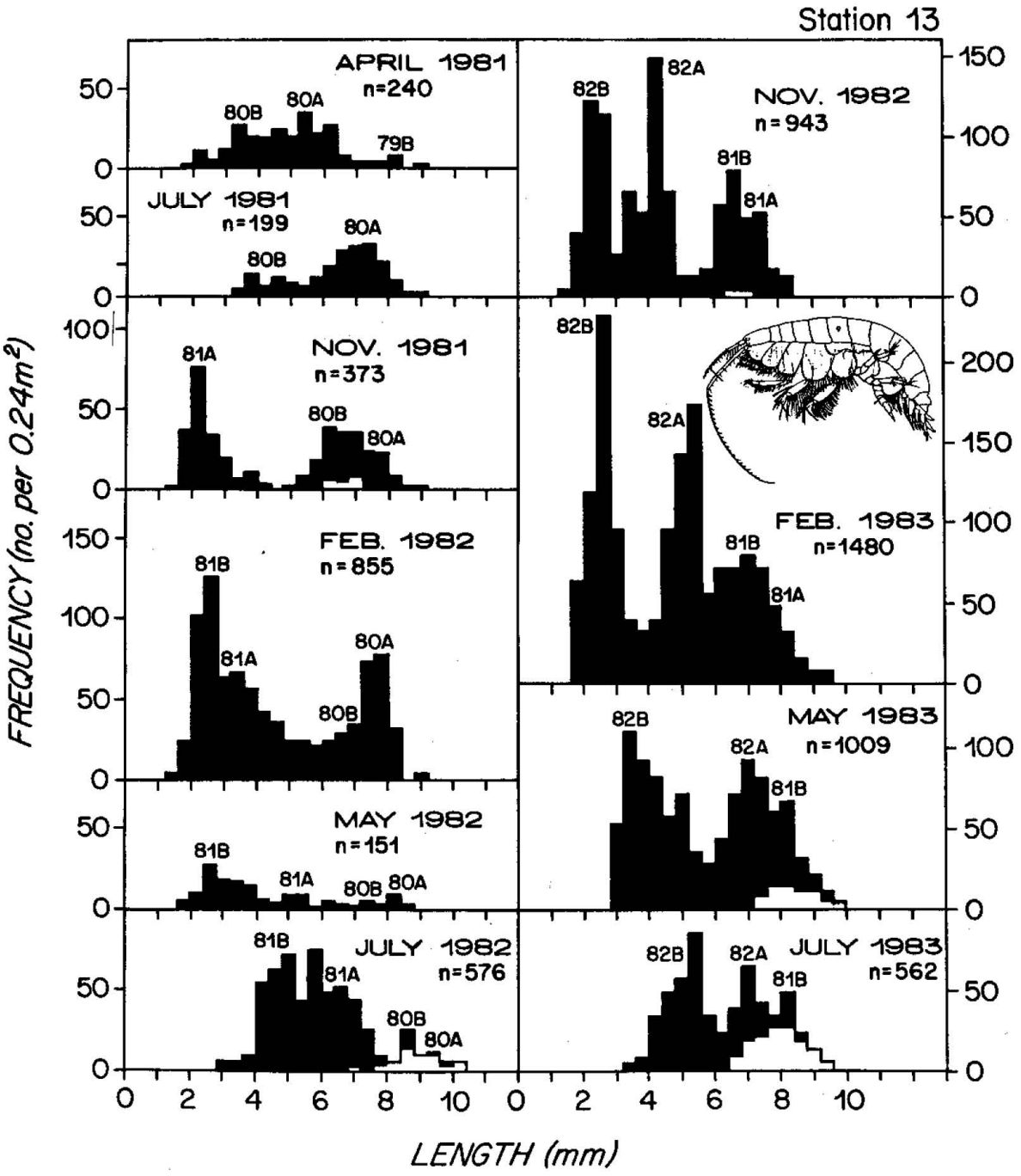


Figure 1-3. Length-frequency of Ampelisca agassizi at Station 13. White blocks in the histograms represent ovigerous females. From Collie (1985).

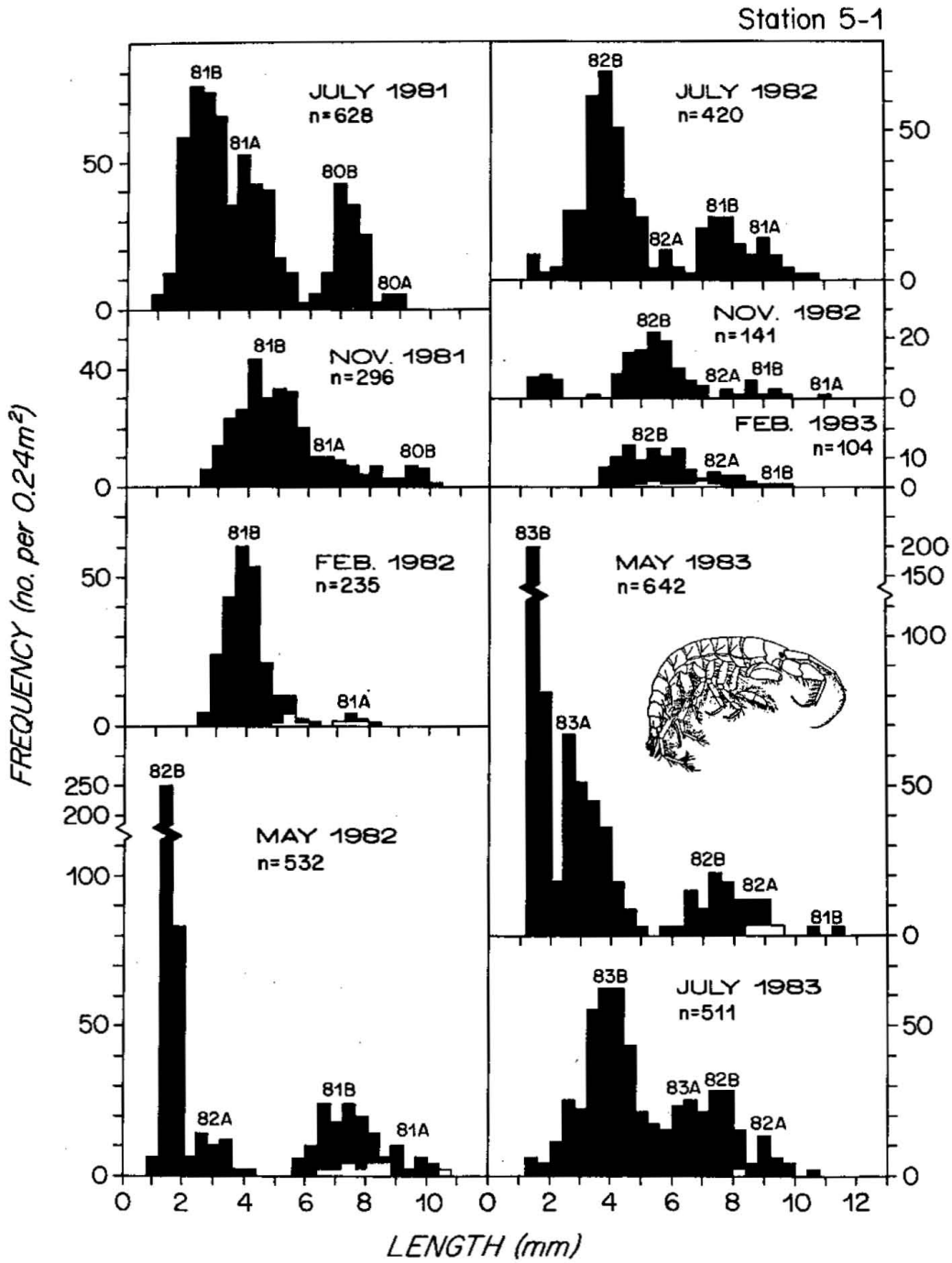


Figure 1-4. Length-frequency of Unciola inermis at Station 5-1. White blocks in the histograms represent ovigerous females. From Collie (1985).

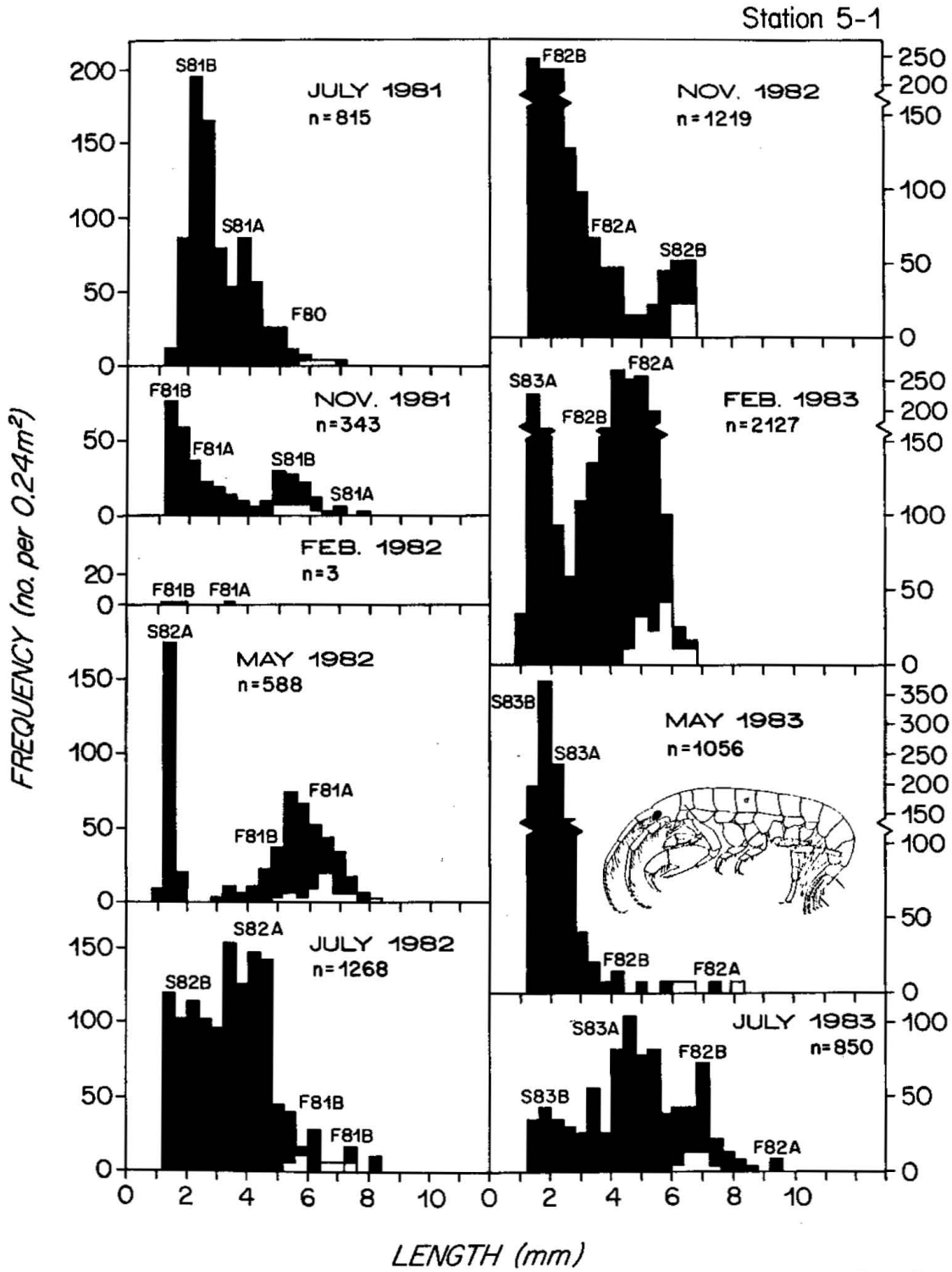


Figure 1-5. Length-frequency of Ericthonius fasciatus at Station 5-1. White blocks in the histograms represent ovigerous females. From Collie (1985).

Unciola inermis at Station 5 (Fig. 1-4) is an annual species with ovigerous females present in February and May (a few in July 1983) and recruitment of juveniles in May. A length of 11 mm may be reached after the maximum life-span of about 1.5 years. The minimum and maximum lengths of ovigerous females were 5.0 and 10.5 mm. A few individuals may survive for a second year (e.g. cohort 81B).

At the same station, ovigerous females of Ericthonius fasciatus (Fig. 1-5) were present throughout the year but recruitment of juveniles was concentrated during the spring and fall, resulting in two generations per year. A striking feature of the distribution of E. fasciatus at this station was its virtual disappearance in February 1982 and subsequent recolonization in May. The reasons for this disappearance and the source of colonists will be discussed below. Animals of the spring generation may reach a maximum length of 7 mm in 6 months; those of the fall generation may reach a maximum of 9 mm in 8 months. Minimum and maximum lengths of ovigerous females were 4.8 and 8.4 mm, respectively.

In all three species, each generation appears to be composed of two modes (these cohorts are labeled A and B in Figs. 1-3, 1-4 and 1-5). Bimodality is more distinct for Unciola inermis and Ampelisca agassizi because their reproduction is more highly synchronous than that of Ericthonius fasciatus. A and B cohorts are apparent for E. fasciatus in July but are less obvious at other times of the year.

To test whether these A and B cohorts are true modes, I ran NORMSEP assuming either one or two modes per generation. In almost all cases, the chi-square was lower with two modes per generation. A and B cohorts were more difficult to separate for adults because, with time, variablity in individual growth rates obscures the modes. Figure 1-6 is an example of the result obtained using NORMSEP to fit the length-frequency

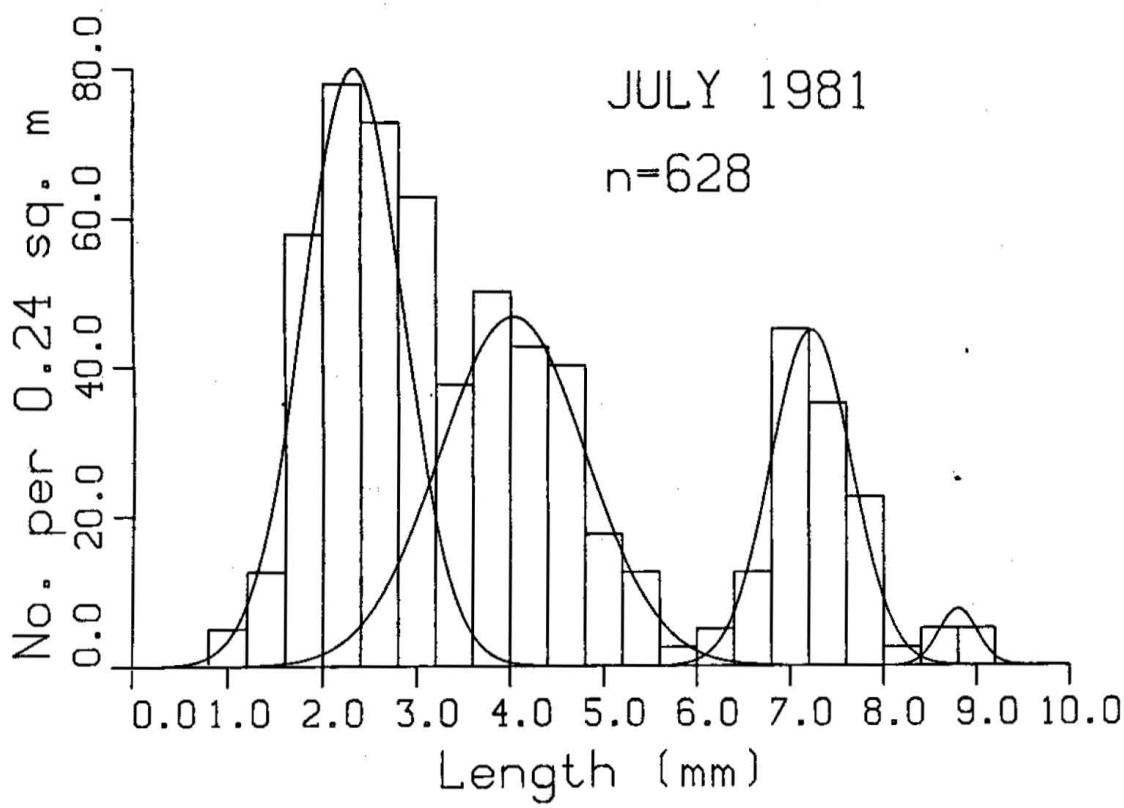


Figure 1-6. Example of the result obtained using computer program NORMSEP to fit normal curves to the observed length-frequency distribution of Unciola inermis at Station 5-1. The chi-square of 4.6 with 8 degrees of freedom indicates that these data fit a group of normal distributions better than 80 percent of samples would be expected to by chance alone. From Collie (1985).

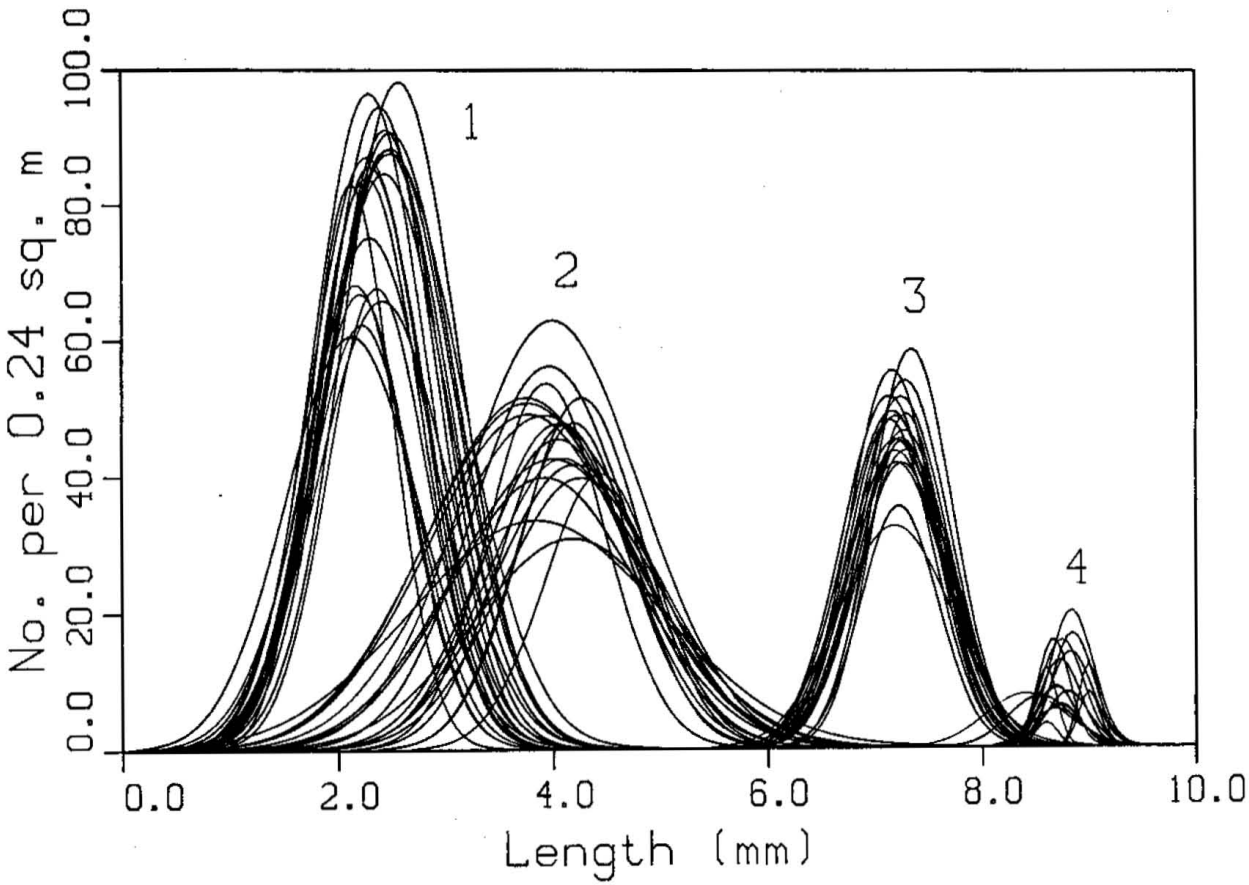


Figure 1-7. Twenty sets of normal curves generated by bootstrap simulation of the Unciola inermis observed length-frequency data plotted in Fig. 1-6.

Table 1-1. Bootstrap parameter estimates corresponding to the normal curves plotted in Fig. 1-7. L_1 are the mean lengths and N_1 the mean numbers of each of the four sets of normal curves shown in Fig. 1-7. The variances of these parameters constitute the diagonal of the variance-covariance matrix.

	VARIABLE							
	L_1	N_1	L_2	N_2	L_3	N_3	L_4	N_4
Observed:	2.32	104.9	4.02	91.7	7.23	48.5	8.80	3.9
Bootstrap:	2.34	105.61	4.02	90.06	7.24	48.59	8.72	4.75

VARIANCE-COVARIANCE MATRIX

L_1	0.018							
N_1	2.100	417.639						
L_2	0.015	2.712	0.027					
N_2	-1.931	-400.452	-2.626	421.999				
L_3	-0.002	-0.264	-0.003	0.274	0.003			
N_3	-0.260	-21.968	-0.053	-14.599	-0.042	40.219		
L_4	-0.004	-0.677	-0.008	0.852	0.001	-0.170	0.022	
N_4	0.091	4.613	-0.034	-6.781	0.030	-3.658	-0.002	5.873

distribution of Unciola inermis in July 1981.

The bootstrap analysis was performed on the observed length-frequency distribution plotted in Fig. 1-6. I simulated 20 sets of length-frequency data and fit NORMSEP in the same manner as the observed data. The 20 sets of normal curves are superimposed in Fig. 1-7; means, variances and covariances of the bootstrap parameter estimates are listed in Table 1-1. Inspection of Fig. 1-7 together with Table 1-1 yields the following insights into this method of size-frequency analysis.

The mean length (L_i) estimates are relatively insensitive to sample variability. This is indicated by the low variances of the L_i parameters in Table 1-1. In contrast, estimated numbers (N_i) in each mode are very sensitive to sample variability. This is illustrated by the large spread in heights of the normal curves and by the high variances of the N_i parameters.

There is a large amount of scatter where modes overlap, for example between modes 1 and 2. This overlap results in the very high negative covariance between N_1 and N_2, the numbers in modes 1 and 2. The overlap also causes positive covariance between L_1 and N_1, L_2 and N_1, and negative covariance between L_1 and N_2, L_2 and N_2. In contrast there is little scatter where modes are distinct, for example between modes 2 and 3. Because these modes are distinct, the covariances among L_2, N_2, L_3 and N_3 are relatively low.

Growth curves for each cohort are shown in Fig. 1-8. The vertical bars equal ± 1 standard deviation as estimated by NORMSEP. Where vertical bars overlap, the modes are indistinct. A common feature of all three species is that the growth rate decreases in the winter; the mean length of Unciola inermis, cohort 81B and 82B, actually decreased between February and May. Ericthonius fasciatus had the fastest growth rate

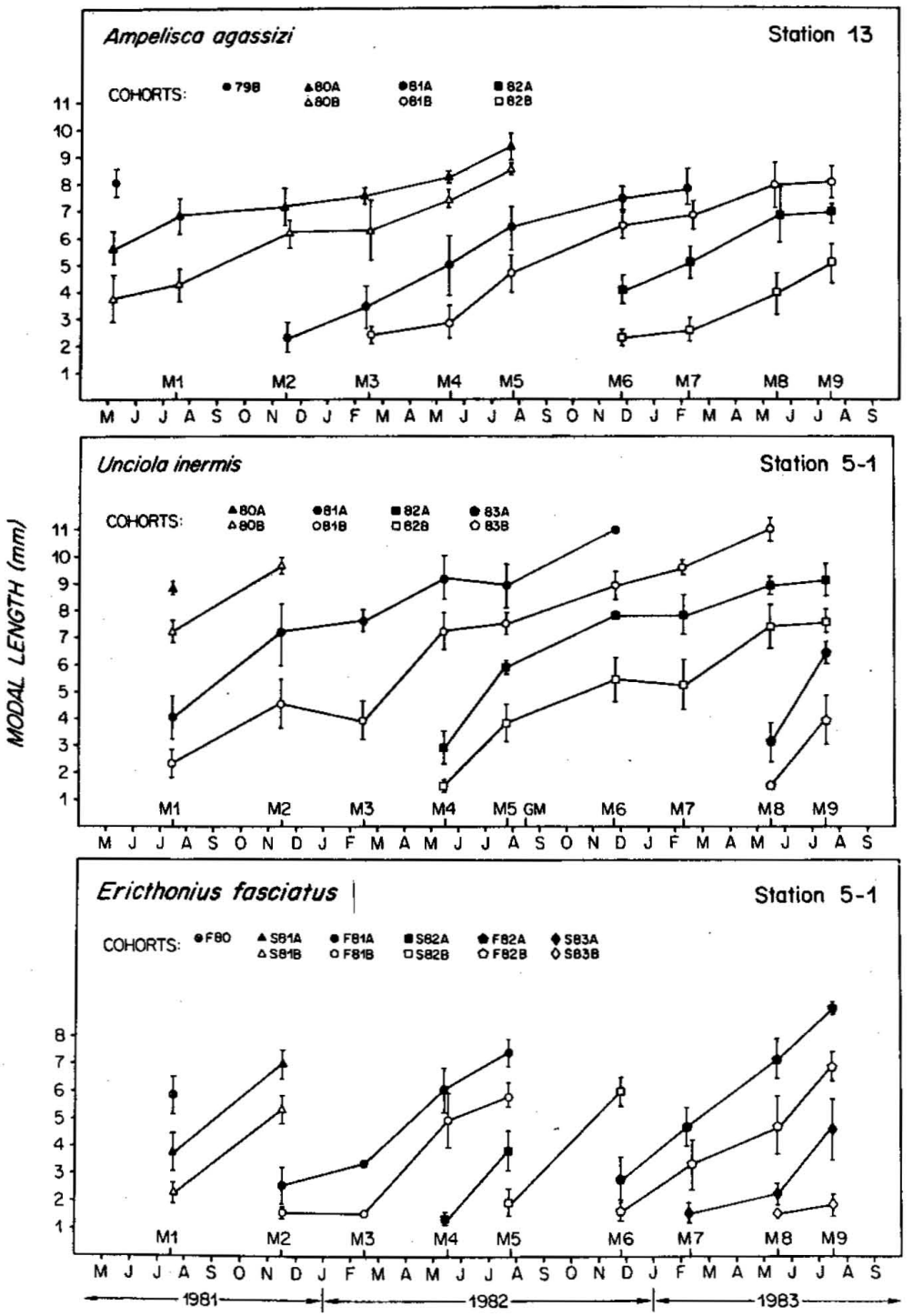


Figure 1-8. Growth in mean length of each cohort. Vertical bars equal ±1 standard deviation as estimated by NORMSEP. From Collie (1985).

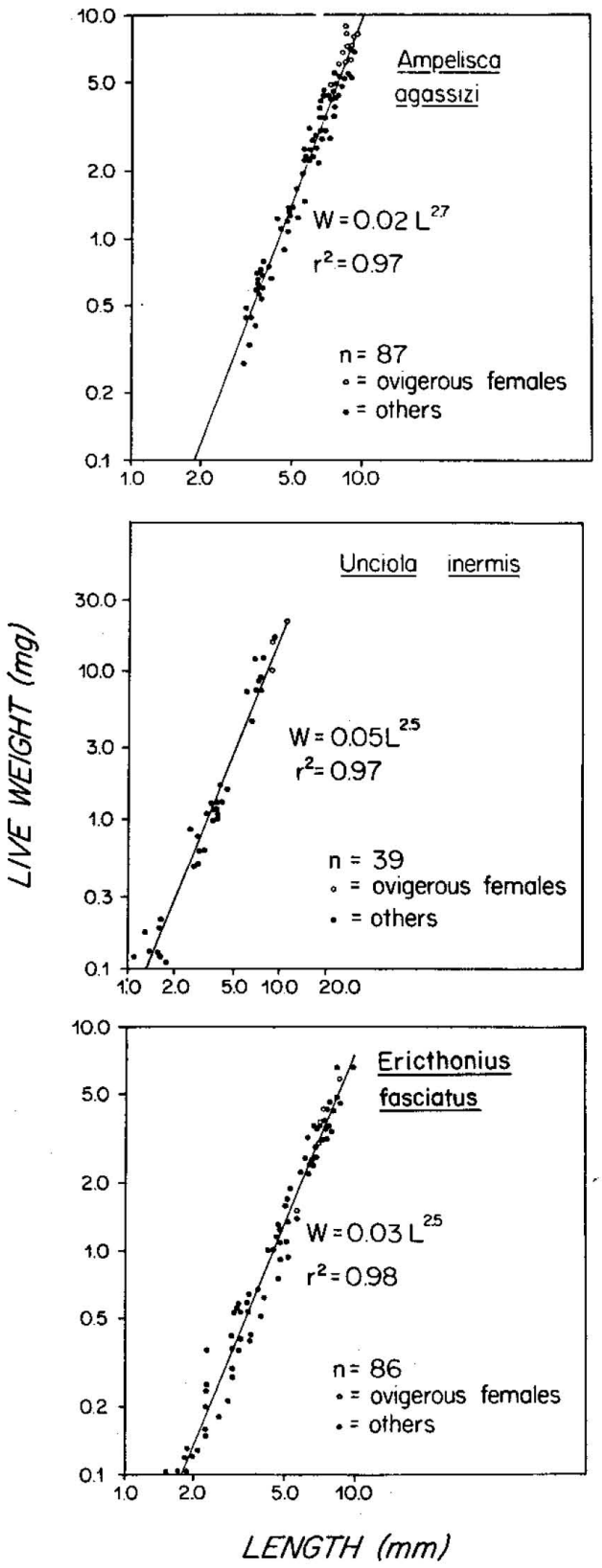


Figure 1-9. Length-weight relationships as fitted by linear least squares. From Collie (1985).

Table 1-2. Ash-free dry weight determination.

Species:	A. agassizi	U. inermis	E. fasciatus
n (groups):	3	3	4
% water:	75.9	74.4	80.9
% ash:	7.1	8.5	6.1
% ash-free dry weight:	17.0	17.1	13.0

Table 1-3. Biomass and production estimates (gdw = grams dry weight).

Species:	A. agassizi	U. inermis		E. fasciatus	
Station:	13	5-1	5-28	5-1	5-28
Production(gdw m^{-2} yr^{-1})					
July 81-July 82	1.26	3.21		1.44	
July 82-July 83	2.79	2.53	2.04	3.12	1.88
July 81-July 83(mean)	2.02	2.87		2.28	
Mean biomass (gdw m^{-2})					
July 81-July 82	0.94	1.20		0.37	
July 82-July 83	1.99	1.19	1.55	0.79	0.67
July 81-July 83	1.48	1.15		0.56	
P/B (yr^{-1})					
July 81-July 82	1.34	2.68		3.89	
July 82-July 83	1.40	2.13	1.32	3.95	2.80
July 81-July 83	1.36	2.50		4.07	

(max. 1mm/mo) with U. inermis intermediate and Ampelisca agassizi the slowest. Thus, there is an inverse relationship between growth rate and life-span.

Length-weight relationships are plotted in Fig. 1-9. Despite the inherent variability of wet weights, a significant regression was obtained for each species by using a relatively large sample size. The regression coefficient (b) of all three species is significantly less than 3. This indicates that growth in weight is not isometric; weight increases less rapidly than does length. Table 1-2 summarizes the ash-free dry weight determinations. Compared to the other two species, Ericthonius fasciatus not only has a lower weight for a given length, it also has a higher percentage of water. This could explain how it grows faster than do the other two species -- by producing less dry weight per unit length.

Production and biomass calculations are given in full in Appendix A and the estimates summarized in Table 1-3. These estimates differ slightly from those presented in Collie (1985) and Collie and Curran (1985) because Eq. 1.1 was used to estimate mean weight in the earlier papers, instead of Eq. 1.2 which is more strictly correct. Ericthonius fasciatus had the highest P/B followed by Unciola inermis then Ampelisca agassizi. Comparing the two years, the P/Bs varied much less than did production and biomass separately. The maximum change in P/B was a 20% decrease by U. inermis; however production and biomass each changed by as much as 2.2 times. Interannual differences in P/B also were less than the differences between species. The Station 5-28 data show that there were between-station differences in production, mean biomass and P/B. Compared to the same species at Station 5-1, amphipods at Station 5-28 grew more slowly and lived longer (growth curves not shown); these

Table 1-4. Sex ratios of Ampelisca agassizi at Station 13.

Date	Grab samples F	M	1:1[1]	Fish stomachs F	M	1:1[1]	guts vs. grabs[2]
July 1982				insufficient numbers			
November 1982							
numbers	24	18	N.S.	21	7	**	N.S.
proportions	0.57	0.43		0.75	0.25		
February 1983							
numbers	57	35	*	73	33	**	N.S.
proportions	0.62	0.38		0.69	0.31		
May 1983							
numbers	92	48	**	109	78	*	N.S.
proportions	0.65	0.35		0.58	0.42		

1. G-test of observed sex ratios against 1:1 ratio.
2. G-test of grab-sample against fish-stomach sex ratios.

Table 1-5. Sex ratios of Unciola inermis at Station 5-1.

Date	Grab samples F	M	1:1[1]	Fish stomachs F	M	1:1[1]	guts vs. grabs[2]
July 1982							
numbers	27	27	N.S.	69	67	N.S.	N.S.
proportions	0.50	0.50		0.51	0.49		
November 1982							
numbers	22	36	N.S.	99	70	*	**
proportions	0.38	0.62		0.59	0.41		
February 1983							
numbers	50	45	N.S.	112	146	*	N.S.
proportions	0.53	0.47		0.43	0.57		
May 1983							
numbers	18	20	N.S.	42	89	**	N.S.
proportions	0.47	0.53		0.32	0.67		

1. G-test of observed sex ratios against 1:1 ratio.
2. G-test of grab-sample against fish-stomach sex ratios.

Table 1-6. Sex ratios of Ericthonius fasciatus at Station 5-1.

Date	Grab samples F	M	1:1[1]	Fish stomachs F	M	1:1[1]	guts vs. grabs[2]
July 1982							
numbers	48	23	**	166	80	**	N.S.
proportions	0.68	0.32		0.67	0.33		
November 1982							
numbers	24	18	N.S.	112	131	N.S.	N.S.
proportions	0.57	0.43		0.46	0.54		
February 1983							
numbers	79	66	N.S.	85	109	N.S.	N.S.
proportions	0.54	0.46		0.44	0.56		
May 1983							
numbers	5	6	N.S	95	115	N.S.	N.S.
proportions	0.45	0.55		0.45	0.55		

1. G-test of observed sex ratios against 1:1 ratio.
2. G-test of grab-sample against fish-stomach sex ratios.

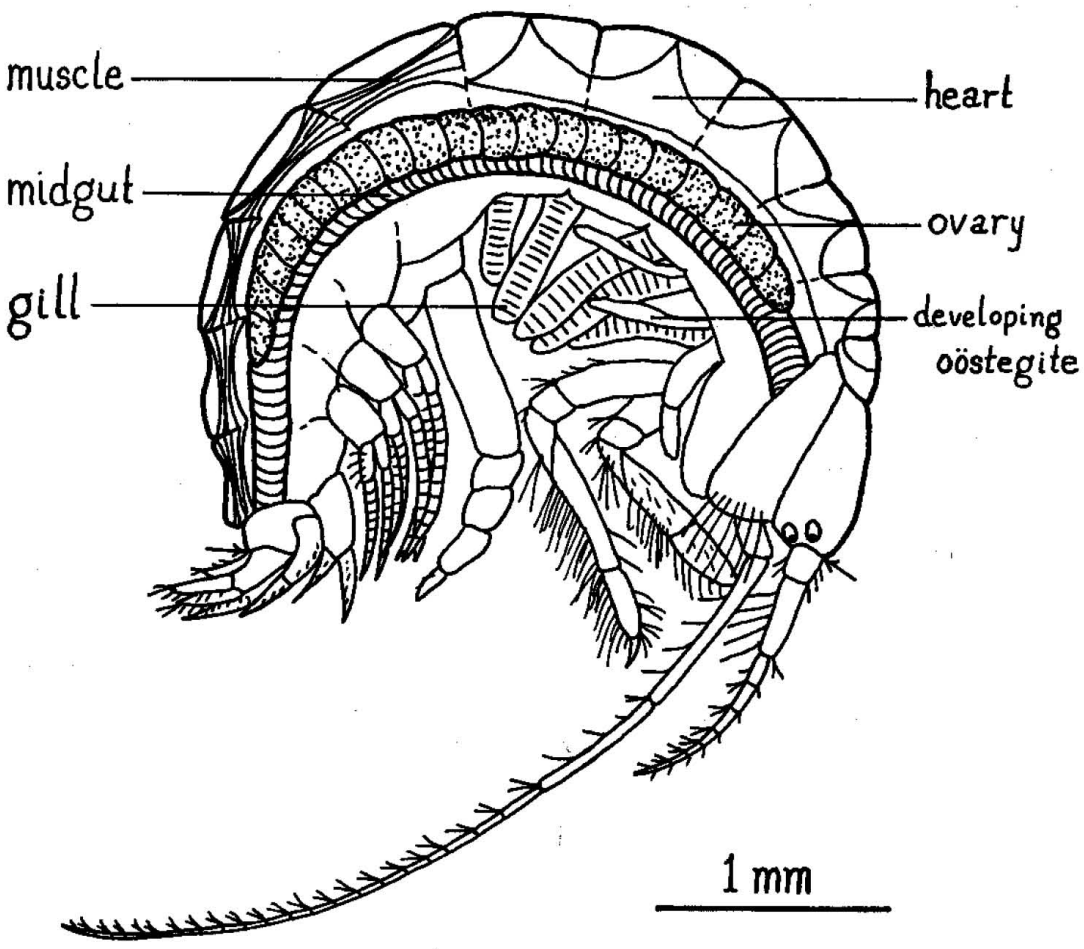


Figure 1-10. Dissection of Ampelisca agassizi. This amphipod, a developing female, was collected at Station 13 in February 1983.

differences account for the lower P/Bs at Station 5-28.

I determined sex ratios of the three amphipod species for the period July 1982 to May 1983 (Tables 1-4 to 1-6). In each case the sex ratio in the grab sample is compared to the corresponding sex ratio of amphipods found in yellowtail flounder stomachs at the same site (see Chapter 2). These sex ratios apply only to the adult (larger than 5 mm) amphipods. The sex ratio of Ampelisca agassizi (Table 1-4) was skewed toward females for both those from grab samples and those from fish stomachs. In no case was the fish-stomach sex ratio significantly different from that of the grab samples.

The sex ratio of Unciola inermis (Table 1-5) from the grab samples was not significantly different from a 1:1 ratio; on 3 out of 4 sampling occasions, the sex ratio from the fish stomachs was different from a 1:1 ratio. In February and May, the fish-stomach ratio was skewed toward males but was not statistically different from the grab-sample ratio. In November the fish-stomach sex ratio was skewed toward females and was significantly different from the grab-sample ratio. In July, the sex ratio of Ericthonius fasciatus (Table 1-6) was skewed toward females both in the grab samples and in the fish stomachs. In no case was the sex ratio in the grab samples significantly different from that in the fish stomachs.

In these amphipod species, the paired ovaries are tubular, with a single row of eggs in each ovary (Fig. 1-10). Sheader (1977) found, in Ampelisca tenuicornis, the length of the mature ovary to be proportional to female body length. If egg size is constant, egg number should be proportional to female body length. In the three species studied here, egg number appears to increase with female length (Figs. 1-11 to 1-13), but this trend is obscured by the scatter in egg numbers. This scatter

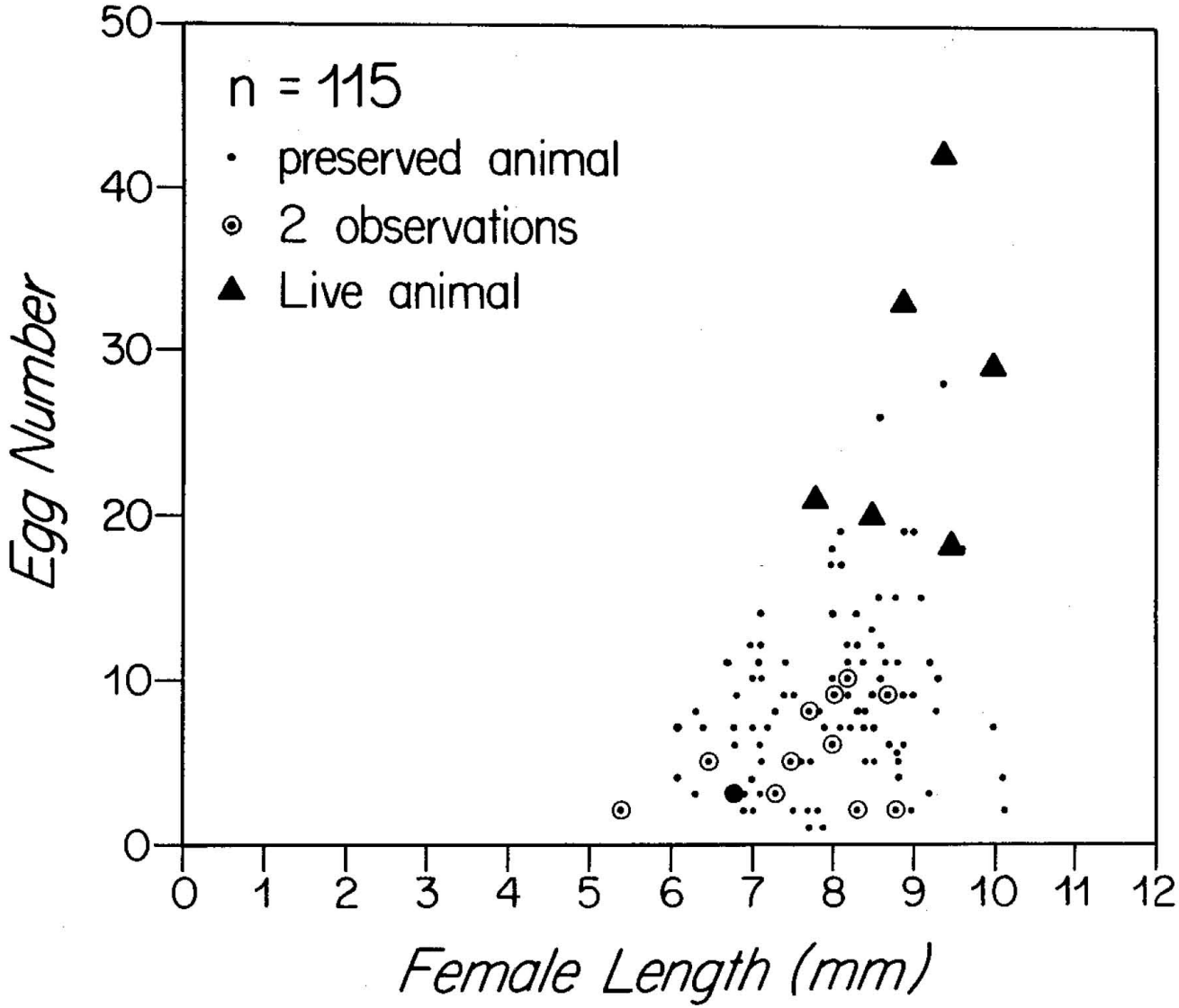


Figure 1-11. Egg number plotted against length of ovigerous Ampelisca agassizi females.

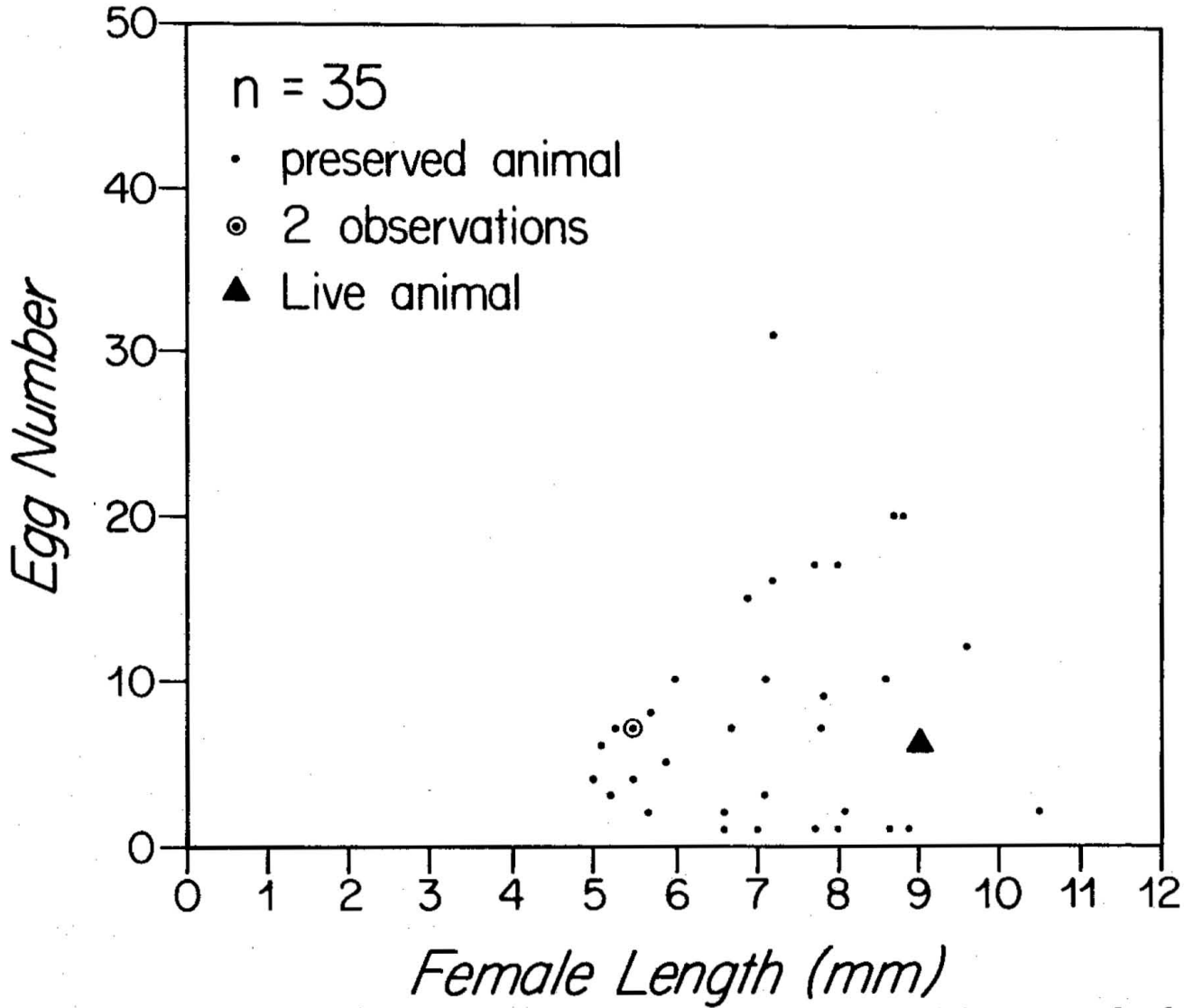


Figure 1-12. Egg number plotted against length of ovigerous Unciola inermis females.

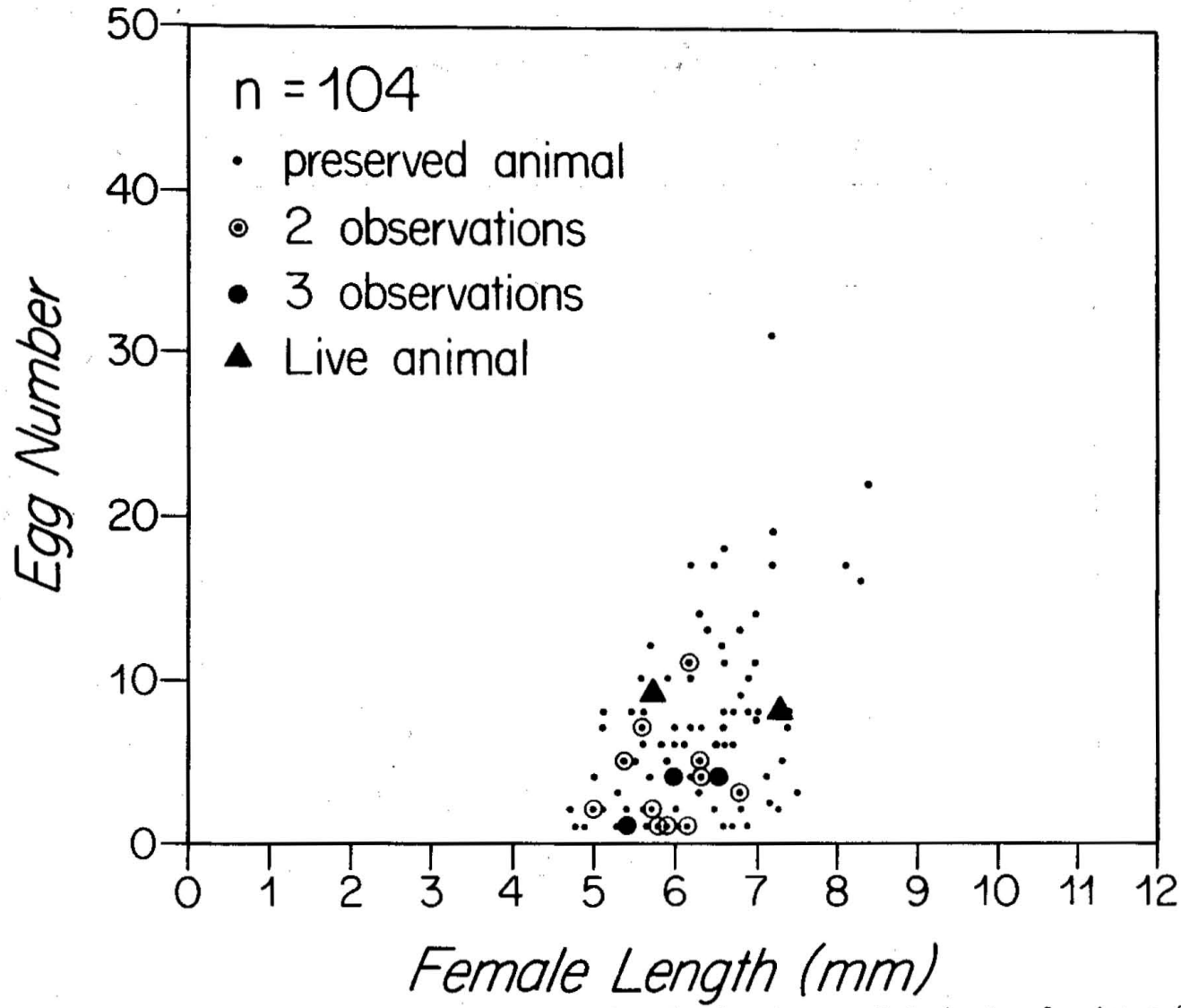


Figure 1-13. Egg number plotted against length of ovigerous Ericthonius fasciatus females.

is probably largely due to egg loss during sample processing. Live A. agassizi (Fig. 1-11) had more eggs than preserved females of equal lengths, probably because the live animals were handled more gently and were less subject to egg loss. Therefore, the maximum egg number in each size class may represent the true fecundity better than mean egg number. More accurate egg counts could be obtained by careful sample treatment or by counting egg number in the ovaries.

I observed parasites in the broods of all three amphipod species. In size and shape the parasite mimics the developing amphipod embryos. The parasite body is pear shaped; a head equiped with two antennae protrudes from a "collar" in the anterior end. The various life stages found in A. agassizi broods (Fig. 1-14) suggest that the life cycle of the parasite is synchronized with that of its host. Some of the parasite bodies appeared distended; I assumed these were in a reproductive state. A large number of parasite eggs are packaged in a transparent ovisac that is the same size as one amphipod egg. The juvenile parasites presumably hatch at the same time as the juvenile amphipods and would thus be able to find a new host without leaving the protection of the brood pouch. The incidence of these parasites was low and presence of a parasite did not appear to interfere with development of the amphipod embryos.

The parasite is difficult to identify because of its globular body form. It is probably a copepod of the family Choniostomatidae (Dr. A. Humes, personal communication). Choniostomatid copepods all parasitise other Crustacea (Bradford 1975) and have been found on at least eight species of ampeliscid amphipods (e.g. Sheader 1977, Dauvin 1984). Adults are thought to be relatively immobile because of the small size of their limbs which are adapted for clinging. All stages have a distinctive sucking mouth cone through which piercing mandibles are extruded,

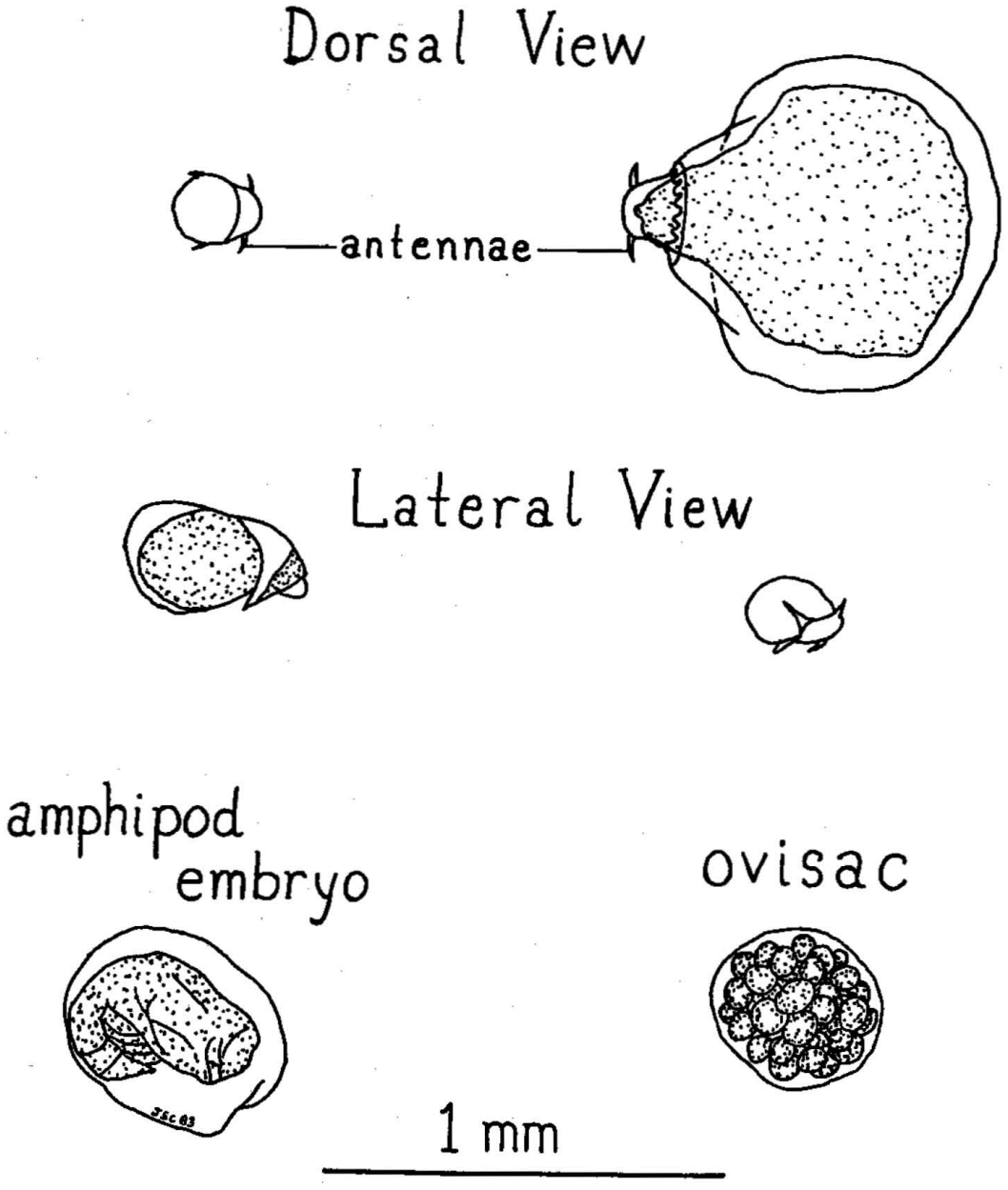


Figure 1-14. Brood parasites on Ampelisca agassizi collected at Station 13 in November 1982. The various parasite stages are shown in relation to a developing amphipod embryo. The parasite is a copepod, probably of the family Choniostomatidae.

presumably enabling them to feed on the blood of their host. The young generally hatch as stage I copepodites and then find a new host.

Table 1-7 compares a number of life-history traits of the three species. The coefficient of variation of sample means is a measure of the patchiness of the species distribution relative to the size of the grab and the area over which the replicates were taken. Thus Ericthonius fasciatus is the most patchily distributed and Ampelisca agassizi the least so. Fish predation data are based on analysis of yellowtail flounder stomachs collected at the same stations (see Chapter 2). Although results given here measure the mean number of prey per predator, not the predation rate, these data suggest that flounder eat E. fasciatus most often and A. agassizi least often.

Table 1-7. Summary of life-history traits (CV = coefficient of variation).

Species:	*A. agassizi*	*U. inermis*	*E. fasciatus*
Generation time:	biennial	annual	semi-annual
P/B (yr^{-1}):	1.3-1.4	1.3-2.7	2.8-4.1
CV of sample means:	40.5	54.8	83.8
Mean no. per fish stom:	15.0	72.4	88.4
Sediment affinity:	fine sand	medium sand	shell fragments

DISCUSSION

The method of length-frequency analysis employed in this study depends critically on the ability to distinguish cohorts and to follow them through time. The three amphipod species considered here lend themselves to this type of analysis because they are relatively short-lived and generations are separable.

Bimodal recruitment has been observed in other amphipod species by other authors. Mills (1967b) found bimodality in both winter and summer generations of Ampelisca abdita. Since the time difference between modes as estimated from the growth curve was about 28 days, Mills suggested that breeding may somehow be linked to the lunar cycle. Corophium volutator, studied by Moller and Rosenberg (1982), has a life history similar to A. abdita. Winter and summer generations are each bimodal and, judging by the authors' Fig. 4, within-generation cohorts are released approximately one month apart. Ampelisca tenuicornis, collected off the northeast coast of England (Sheader 1977), also exhibits bimodal generations. Sheader suggested that this recruitment pattern results from the simultaneous onset of breeding and the synchronous production of a second brood by a proportion of the females. The following spring the first brood matures earlier than the second, thus reinforcing the double peak of recruitment. Dauvin (1984) found multimodal recruitment (up to 11 cohorts per generation) in A. typica, A. sarsi and A. tenuicornis.

For the three amphipod species I studied, the cue for the onset of breeding is not apparent because ovigerous females of at least one species were present during all seasons of the year. Onset of breeding is a function of length in that the cohorts mature sequentially with the largest females maturing first. This tends to reinforce the bimodal

recruitment but probably is not enough, in itself, to maintain the pattern.

Sheader (1977), Dauvin (1984) and Kemp et al. (in press) found females carrying embryos in their marsupia and, simultaneously, well-developed oocytes in the ovaries; it is likely that some of these females bred a second time. The development time for ampeliscid embryos ranges from 1 month in A. tenuicornis (Sheader 1977) and A. sarsi (Dauvin 1984) to 5 months in A. macrocephala (Kanneworff 1965). In my study, some cohorts had ovigerous females on two consecutive sampling dates, suggesting that multiple broods are possible. The development time for embryos of these species is not known. In developing females the ovaries were clearly visible (Fig. 1-10) but none of the ovigerous females observed also had developing oocytes.

In ampeliscid amphipods, males mature at a definitive last moult that almost amounts to a metamorphosis. The modifications during this terminal moult, which include slimming of the body and increase in pleon muscle size, are associated with improved swimming ability and adaptation for a short, free-swimming, adult life (Mills 1967b).

In several studies of ampeliscid life history, the density of adult males declined, following the breeding season in early summer, to almost zero by the end of the summer. This pattern was observed in A. macrocephala (Kanneworff 1965), A. tenuicornis (Sheader 1977) and A. brevicornis (Klein et al. 1975, Hastings 1981a). The males are presumed to leave the bottom as they mature. In night-time plankton hauls Hastings (1981a) found only mature, metamorphosed male A. brevicornis and these pelagic males had spermatophores extruding from the penes. In contrast, Mills (1967b) found all stages of A. abdita, from juveniles to fully adult males and females, in night-time plankton tows in Barnstable

Harbor. Interestingly, the sex ratio of A. abdita was roughly 1:1.

The sex ratios of A. agassizi are complicated by the presence of intersexes: animals with penile papillae and rudimentary oostegites. Such intersexes, also observed in A. brevicornis (Hastings 1981a), A. spinipes (Mills 1963) and A. macrocephala (Kanneworf 1965), have been called gynomorphic males. Hastings (1981b) made a histological study of five intersex A. brevicornis. All five were confirmed as males by the presence of immature testicular tissue and all five were infested with internal parasites. This phenomenon, which appears to be a form of parasitic castration, is widespread throughout the crustacea. In A. agassizi 4% of all identified males were gynomorphic.

Mature male A. agassizi were present in May; the percent of males that were mature was slightly higher in the fish stomach contents (15%) than in the grab samples (12%). As the adults matured, from November to May, the proportion of males decreased in the grab samples and increased in the fish stomachs. This observation is consistent with the hypothesis that males leave the bottom as they mature and are then more vulnerable to fish predation. This trend, however, was slight and did not significantly alter the sex ratios, which remained skewed toward females at all seasons.

The proportion of male Unciola inermis in the diet increased from November to May as the adults matured, suggesting that mature males enter the water column and are more prone to predation. Again, this trend was slight and didn't appear to drive the sex ratio in the benthos away from a 1:1 ratio.

Because Ericthonius fasciatus is capable of year-round reproduction, there is no prediction of how the sex ratio should change. The sex ratio in the fish stomach contents mirrored that in the grab samples. Of the

three species, E. fasciatus is the most epibenthic in habit. Together, these observations suggest that both sexes are equally vulnerable to fish predation. In summary there is some evidence that mature males of A. agassizi and U. inermis leave the sea bottom but this pelagic habit does not make them significantly more vulnerable than females to predation by yellowtail flounder.

Comparison of the life-history strategies of the three amphipod species (Table 1-7) yields a consistent pattern. Ampelisca agassizi is mainly a deposit feeder on fine sediments in weak curents; its tube extends vertically in the substratum, providing a refuge from fish predation. Of the three species, A. agassizi has the slowest growth, lowest mortality and is eaten least by flounder. The low turnover rate and less patchy distribution could be related to this species' affinity for finer sediments at greater water depths where the sediments presumably are disturbed less frequently.

In contrast, Ericthonius fasciatus is an epifaunal tube builder, living in stronger currents, perhaps mainly as a filter feeder. Among the three species, E. fasciatus has the fastest growth, highest mortality and is eaten most by flounder. The high turnover rate and patchier distribution of this species may be related to its affinity for coarser sediments at shallower depths where sediment resuspension presumably is more frequent. Unciola inermis is also an epifaunal tube-builder in moderate currents but tubes are usually built into the substratum and are thus less exposed to predation. The life-history traits of U. inermis are intermediate among the three amphipod species.

Frequency of sampling was dictated by the GBMP and thus could not be controlled in this study. While more frequent sampling would increase the precision of the production estimates, I do not think any

reproductive events were missed by the sampling regime. My estimates do not account for the production of a cohort before the first date or after the last date it appears in the samples. This underestimate should be small compared with the total production of the cohort over its life-span because, in the first case the mean weight of individuals is small, while in the latter case the numbers are few.

To calculate the maximum potential production underestimate, I made the following assumptions. For a juvenile cohort first sampled at Q(t), I assumed that the entire cohort recruited immediately following the sampling date, Q(t-1), when the cohort was not present. The lengths of these recruits were assumed to be the same as the lengths of newly recruited juveniles of each species. For adult cohorts that disappeared following Q(t), I assumed that the entire cohort lived until immediately before the next sampling date, Q(t+1), and that the mean length was equal to the greatest mean length observed for that species.

Using these assumptions I recalculated production for the two-year period. Maximum potential production underestimates were 7.2% for Unciola inermis, 17.2% for Ampelisca agassizi and 50% for Ericthonius fasciatus. The potential underestimate for U. inermis is probably smaller than errors from other causes. For A. agassizi the potential underestimate is largely accounted for by the disappearance of the 81A cohort after February 1983 and the 82A cohort not appearing in the samples until a mean length of 4 mm. The large potential underestimate for E. fasciatus is mostly due to the untimely disappearance of cohort S82A after July 1982. These assumptions are for the worst-case scenario; the actual production underestimates are almost certainly less. For annual species, quarterly sampling is probably adequate; for semi-annual species more frequent sampling (e.g. every two months) would be desirable.

Errors in estimating the number of animals in each cohort could be the result of migration, patchiness in species distribution, variation in sampling efficiency, or from using the computer program NORMSEP. It is not always possible to distinguish these sources of error, so I shall discuss only the most glaring numerical inconsistencies.

The total number of Ampelisca agassizi decreased sharply in May 1982 and then increased in July 1982 even though there was no recruitment during this period. Of the three species considered here, A. agassizi is the least patchy and least mobile, suggesting that this inconsistency is a sampling problem. In May 1982 owing to heavy seas, the grab samples were taken slightly west of the true station coordinates (Battelle and WHOI 1985, Appendix A). Station 13 appears to be located on a sharp gradient in species abundance, increasing from west to east.

On the other hand, the virtual disappearance of Ericthonius fasciatus in February 1982 does not seem to be a sampling problem because Unciola inermis persisted in the same grabs. Reappearance of E. fasciatus in May 1982 was probably due to colonization by adults from adjacent areas where this species had remained abundant. The following February E. fasciatus reached its highest density. In a population open to migration, production is lost and gained to and from other areas. Therefore, production as estimated here does not apply to a closed population but instead applies to the area of sea bottom over which the samples were taken.

The results of the bootstrap analysis agree closely with those of an independent test performed by McNew and Summerfelt (1978). These authors used NORMSEP to estimate mean length-at-age and percent composition of the component age groups in 10 collections of largemouth bass for which age was determined by counting growth rings on scales. Compared to fish

aged by the scale method, the error of the estimated mean length-at-age averaged 3.2%. About one-third of the frequency distributions deviated significantly from a normal distribution but this lack of fit did not greatly influence accuracy in estimating mean length. The average error of the estimated percent composition-by-age was 28%; the magnitude of this error was related to the degree of asymmetry in the distribution and a large standard deviation of length.

In my bootstrap trials the coefficient of variation of mean length ranged from 1.7 to 5.6; the coefficient of variation of numbers ranged from 12.7 to 51.0. Obviously mean lengths can be estimated with more confidence than numbers. This is not surprising because the length ewtimate varies in only one dimension while the estimated number (the area under the normal curve) also reflects the variability of the estimated standard deviation. Consequently, growth rates derived from length-frequency data are more reliable than corresponding mortality rates. Growth rates and mortality rates are required to estimate production. If a bootstrap analysis were performed for each sample date, the variance of the production estimate could be obtained by calculating the production of each simulated cohort. Alternately, an analytical formulation of the variance could be derived, based on the variances and covariances of all parameters in the production equation.

Despite the qualifications mentioned above, these are the first direct production estimates for benthic macrofaunal species on Georges Bank. Table 1-8 lists production estimates of various species of marine amphipods from various locations. For ease of comparison all production rates are given in units of grams dry weight m^{-2} yr^{-1}. Where the appropriate conversion factor was not given by the author(s), I used my percent-composition data from Table 1-2. I used the data for Ampelisca

Table 1-8. Annual production estimates of marine gammaridean amphipods (gdw = grams dry weight).

Family Species	Location and depth (meters)	Production (gdw m^{-2} yr^{-1})	P/B (yr^{-1})	Generations per year	Life-span (months)	Reference
Ampeliscidae						
Ampelisca complex[a]	Long Island Sound (18)	1.4	5	2	6	Sanders (1956)
A. spinipes	Bay of Concarneau, Brittany (17)	0.2	2.4	1	24	Glemarec & Menesguen (1980)
A. tenuicornis	North Sea (58)	0.2[b]	3.4	1	12-15	Sheader (1977)
A. tenuicornis	Bay of Morlaix, Brittany (25)	0.7	3.1	2	16	Dauvin (1979)
A. tenuicornis	Rance Maritime, Brittany (4)	0.7-1.7	3.7-4.2	2	16	Dauvin (1984)
A. typica	Bay of Morlaix, Brittany (25)	.07	4.0	2	12-16	Dauvin (1984)
A. brevicornis	Bay of Morlaix	.04[c]-0.2	2.2[c]-2.7	2	12	Dauvin (1979,1984)
A. brevicornis	Rance Maritime, Brittany (4)	0.2-0.5	2.6-2.8	2	12	Dauvin (1984)
A. brevicornis	Bay of Concarneau, Brittany (17)	4.1	2.5-4.8	?	?	Menesguen (1980) in Dauvin (1984)
A. brevicornis	North Sea (28)	0.3-0.7	3.1-4.8	1	15	Klein et al. (1975)
A. brevicornis	Isle of Man (intertidal)	1.3-1.7	2.5-3.2	1	15	Hastings (1981a)
A. araucana	Coast of Chile (65)	5.8[d]	1.9[d]	2	7	Carrasco & Arcos (1984)
A. armoricana	Bay of Morlaix, Brittany (25)	9.7	2.6	1	18-24	Dauvin (1979)

Table 1-8 cont.

Family Species	Location and depth (meters)	Production (gdw m^{-2} yr^{-1})	P/B (yr^{-1})	Generations per year	Life-span (months)	Reference
Ampelscidae cont.						
Ampelisca sarsi	Bay of Morlaix, Brittany (25)	.01[d]–0.9	1.7[d]–2.4	1	21	Dauvin (1979,1984)
A. agassizi	Georges Bank (69)	1.3–2.8	1.3–1.4	1	24	This study
Haploops fundiensis	Bay of Fundy (80)	0.1[b]	1.3	0.5	27	Wildish (1984)
Aoridae						
Unciola inermis	Georges Bank (84)	2.0–3.2	1.3–2.7	1	18	This study
Corophiidae						
Corophium insidiosum	Corsica (brackish)	3–60	12–19.5	3+	1–2	Casabianca (1975)
C. insidiosum	Swedish coast (intertidal)	0.2–8.4[e]	3.0–4.9[e]	3+	4	Birklund (1977)
C. volutator	Swedish coast (intertidal)	2.5–3.8[e]	3.2–4.4[e]	3+	3	Birklund (1977)
C. volutator	Swedish coast (intertidal)	1.5–24[b]	5.1–11.3	2	6	Moller & Rosenberg (1982)
C. volutator	Thames River Estuary (?)	95.6	7.7	?	?	Mossman (1978) in Moller & Rosenberg (1982)
C. salmonis	Coast of Washington (?)	3.6–10.7	7.2–8.6	3+	?	Albright & Armstrong (1982)
Haustoridae						
Haustorius canadensis	Coast of Maine (intertidal)	1.5[b]	1.5	0.5	24	Donn & Croker (1983)
Ischyroceridae						
Ericthonius fasciatus	Georges Bank (84)	1.4–3.1	2.8–4.0	2	6–8	This study

Table 1-8 cont.

Family Species	Location and depth (meters)	Production (gdw m^{-2} yr^{-1})	P/B (yr^{-1})	Generations per year	Life-span (months)	Reference
Melitidae						
Casco bigelowi	Bay of Fundy (80)	0.3[b]	2.5	1	18	Wildish (1984)
Photidae						
Photis reinhardi	Bay of Fundy (80)	0.1[b]	2.8	1	18	Wildish (1984)
Phoxocephalidae						
Harpinia propinqua	Bay of Fundy (80)	.02[f]	3.1	1	14	Wildish (1984)
Rhepoxynius abronis	Coast of Oregon (5)	0.7-1.1	1.3-2.1	1	18	Kemp et al. (In press)
Pontoporeiinae						
Pontoporeia affinis	Baltic Sea (46)	1.9-4.4	1.2-2.6	0.5	36	Cederwall (1977)
P. femorata	Baltic Sea (46)	1.4-4.6	0.8-2.1	0.5	36	Cederwall (1977)
P. femorata	Nova Scotia (4-10)	2.8-3.4[b]	3.6-4.8	1	12-18	Wildish & Peer (1981)
Urothoe brevicornis	Isle of Man (intertidal)	1.3-1.9	0.9-1.6	0.5	?	Hastings (1980) in Hastings (1981a)
Talitridae						
Talorchestia margaritae	Coast of Venezuela (beach)	660[g]	29.2[g]	3+	3	Venables (1981)

a. A. diadema, A. spinipes, and A. tenuicornis.
b. These values were converted to gdw using percent composition data in Table 1-2.
c. These values were affected by the Amoco Cadiz oil spill.
d. These values were recalculated from Table 1 of Carrasco and Arcos (1984).
e. Production was calculated from May to September.
f. This value was converted to gdw using percent composition data for R. abronis (Kemp et al. In press)
g. Extrapolated from mean daily production.

agassizi for all ampeliscids, and Ericthonius fasciatus data for Corophium. For other species, I assumed dry weight to equal 25% of wet weight.

Compared to other ampeliscids having one generation per year, Ampelisca agassizi has a lower P/B but an intermediate production rate by virtue of its higher mean biomass. Since Unciola inermis and Ericthonius fasciatus are in the superfamily Corophioidae, they should be compared to Corophium. Production of U. inermis and E. fasciatus is within the range of estimates for the intertidal corophid species. Apparently, amphipod production on Georges Bank is as high as production by related near-shore species of similar life-span.

Results of this study have implications for pollution monitoring. Most of the observed variation in amphipod numbers can be accounted for by recruitment and subsequent natural mortality. The observation that P/B varied less than did density, biomass or production alone suggests that this ratio may be useful in monitoring the effects of pollution on marine communities. Using this method, it presently is not possible to say whether two P/Bs are statistically different. A means of calculating confidence intervals for the production estimates is needed.

CHAPTER TWO

FOOD SELECTION BY YELLOWTAIL FLOUNDER

INTRODUCTION

In this part of the study I analyzed the food habits of the yellowtail flounder, Limanda ferruginea (Storer), as they relate to the distribution and abundance of benthic prey species. Fish stomachs collected by the Northeast Fisheries Center (NEFC) concurrently with benthic sampling by the Georges Bank Benthic Monitoring Program (GBMP) enabled me to compare ingested and available food. I analyzed these data, the first of their kind for yellowtail flounder and for any fish species on Georges Bank, to determine whether predation patterns are predictable with respect to prey species and prey size.

Although the food habits of many fish species have been studied by examining the fishes' stomach contents (e.g. Verrill 1871, Kendall 1898), much of this information is qualitative and even anecdotal in nature. Few studies considered prey selection in relation to prey availability and fewer still tested for size-selective feeding. Existing food habits data give a static description of what eats what. Detailed and quantitative studies will lead to a better understanding of the dynamic interactions between fish and their prey.

The yellowtail flounder is a right-handed, small-mouthed flounder (Fig. 2-1) that occurs along the eastern seaboard of North America from Labrador to Chesapeake Bay, at depths of 10 to 100 m (Bigelow and Schroeder 1953). It has contributed significantly to the commercial flatfish catch, primarily from southern New England and Georges Bank, since about 1935 (Clark et al. 1984). The biology and distribution of

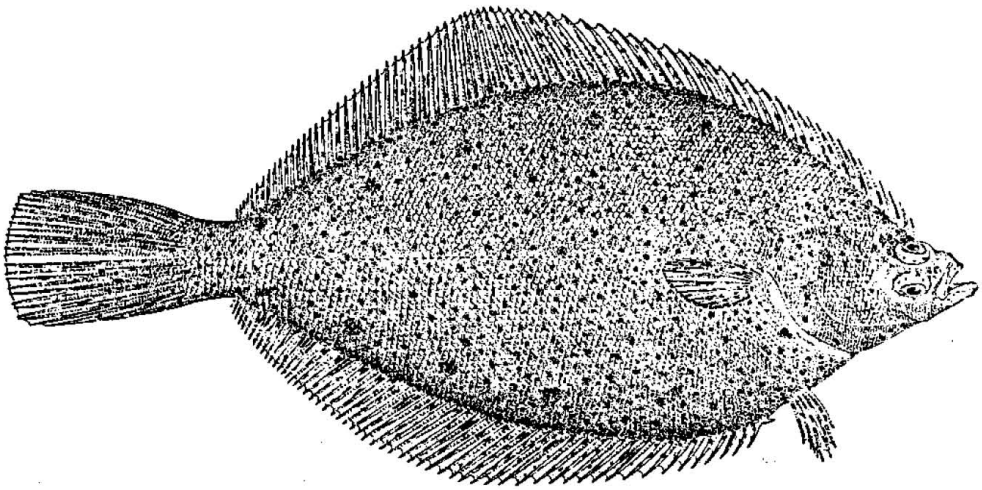


Figure 2-1. Yellowtail flounder, Limanda ferruginea (Storer). From Bigelow and Schroeder (1953). Drawing by H.L. Todd.

yellowtail flounder were recently summarized by Lux and Livingston (1982). Yellowtail usually spawn for the first time when they are three years old and about 30 to 35 cm long. The small mouth, with a single row of fine teeth and pronounced downward orientation, is adapted for benthivory.

Previous studies of yellowtail flounder food habits all showed that polychaetes and amphipods constitute the bulk of the diet. Yellowtail flounder feeding was studied by Efanov and Vinogradov (1973) on Southern New England and Georges Bank, by Pitt (1976) on the Grand Banks and by Libey and Cole (1979) off Cape Ann, Massachusetts. Langton and Bowman (1981) analyzed the food habits of eight pleuronectiform fish, including yellowtail flounder, collected on groundfish survey cruises from 1969 to 1972. A more detailed study was made of fish stomachs collected on survey cruises from 1973 to 1976 and the data were analyzed separately by Langton (1983) and Bowman and Michaels (1984). The yellowtail flounder diet changed with length, in that polychaetes were increasingly more important in larger fish and amphipods less so. The major prey species were polychaetes (Spiophanes bombyx, Spionidae, Lumbrineridae and Nephtydae), amphipods (Unciola spp., Byblis serrata and Leptocheirus pinguis), and decapods (Crangon septemspinosa and Dichelopandalus leptocerus).

Electivity indices measure the utilization of food types (r) in relation to their abundance or availability in the environment (p). Foods constituting a larger proportion of the diet than of the available food are considered preferred; conversely, those proportionately under-represented in the diet are considered avoided. A food is eaten at random if its proportion in the diet equals its proportion in the environment. A family of electivity indicies exist, that are related

mathematically and differ only in the particular algorithm used to calculate electivity from r and p.

Lechowicz (1982) graphed the values of each electivity index as contours for all combinations of r and p. He compared the strengths and weaknesses of each index with the following criteria: 1) the index value when r=p for a food; 2) the symmetry of electivity as feeding deviates from random; 3) the possible range of index vlues; 4) the linearity of changes in electivity over the full range of r and p; 5) the sensitivity of the index to sampling errors; 6) the statistical testability of electivity; and 7) the stability of the index for a food type that either changes in relative abundance or occurs in combination with different food types. No one index ideally satisfies all the criteria; different indices may be appropriate in different situations.

The next section briefly reviews studies in which fish stomach contents were analyzed in relation to prey abundance, with particular attention to methodological advances relevent to this thesis. (Food selection by demersal fish seems to be a recurring theme of graduate research -- seven of the following studies are theses or were excerpted from theses.) Smith (1950) studied the food habits of eight demersal fish species in Block Island Sound. Species abundance in benthic samples was too low to calculate an index of selection.

Ivlev, in experiments reported in his classic (1961) monograph, studied food selection, mainly by carp held in captivity and feeding in a variety of conditions. Ivlev's index of electivity (E), which has been widely used in other studies, is:

$$E_i = (r_i - p_i)/(r_i + p_i) \qquad (2.1)$$

where r_i and p_i are, respectively, the proportions of prey species i in the diet and environment. The advantages of E are that it is bounded between +1 and -1 and it is symmetrical about the neutral value of 0. The disadvantages are that changes in E are not linear, it is not stable if prey abundance changes, and it is not amenable to statistical testing.

Levings (1974) studied the food habits of winter flounder (Pseudopleuronectes americanus) in St. Margarets Bay, Nova Scotia. Comparing the species compositon of stomach contents to that in Ekman grab samples, he calculated E values for different size classes of prey. Above a threshold size, there was a close correspondance between the size spectra of available and ingested prey. Frame (1974) studied the feeding habits of young winter flounder in a Massachusetts estuary. He calculated percent overlap between the volumes of prey species in fish stomachs and in Peterson grab samples. Percent overlap increased during the year as winter flounder made the transition from pelagic to benthic feeding.

Gabriel and Pearcy (1981) studied the feeding selectivity of Dover sole (Microstomus pacificus) off the Oregon coast. They calculated Ivlev's E based on the numbers of different prey species in fish stomachs and in serially sectioned box-core samples. Prey selection was tested statistically with chi-square contingency tables. Larger sole ate larger prey and prey found deeper in the sediment. Sedberry (1980) studied the food habits of a community of fish in the Middle Atlantic Bight. He calculated Ivlev's E based on the numbers of different prey species in fish stomachs and in Smith-McIntyre grab samples.

In his extremely comprehensive thesis, Dauvin (1984) analyzed the stomach contents of demersal fish on the coast of Brittany, but attempted no quantitative comparison between stomach contents and benthic samples

collected in the same area. MacDonald (1982) studied the food habits of five benthivorous fish species in Passamaquoddy Bay, New Brunswick. He used three-factor multiple analysis of variance (MANOVA) to test for overall significant differences in prey species composition among the five fish and Ponar grab samples, at two sites, on seven dates in one year. Using, discriminant functions analysis he assessed diet overlap and overlap between stomach contents and benthic abundance.

Schmitt and Holbrook (1984a, 1984b) studied prey selection by black surfperch (Embiotoca jacksoni) and striped surfperch (E. lateralis) feeding on invertebrates found on benthic turf and foliose algae. These authors compared the taxonomic composition of stomach contents to that of available prey but did not calculate a prey-selection index. Using, Chesson's (1978) α index they compared the sizes of available and ingested prey. This index is calculated as the forage ratio weighted by the sum of all forage ratios:

$$\alpha_i = (r_i/p_i)/\sum_{k=1}^{n}(r_k/p_k) \quad . \qquad (2.2)$$

Here, i refers to the various prey size classes. Alpha varies exponentially from 0 to 1; neutral selection corresponds to 1/n, where n is the number of prey categories. The advantages of α are that it is insensitive to changes in prey abundance and it is approximately multivariate normally distributed. These properties enabled Schmitt and Holbrook to use MANOVA for comparing size selection between the two surperch species and among different size classes of black surfperch.

The studies reviewed above measured either species selection or size selection; none explicitly investigated the interaction between species and size preference. Andersen (1982) formulated a mathematical treatment

of fish-stomach contents, in relation to prey abundance, which accounts for both species and size selection. Andersen's suitability coefficient (G_{ij}) is the product of a species coefficient (ρ_i) and a size-preference coefficient (g_{ij}). The species coefficient (ρ_i) is, by definition size-independent; g_{ij} is theoretically a lognormal function of the predator-to-prey weight ratio and may or may not be the same for different prey species. I shall show in the methods section that the suitability coefficient (G_{ij}), when normalized to unity, is exactly equivalent to the alpha index calculated over prey species and prey size (α_{ij}).

Ursin (1981) interpreted Andersen's mathematical formulations and discussed the requirements for fitting Andersen's model to field data. This model requires very complete data; in only a few cases has it been applied to field data. Arntz and Ursin (1981) analyzed the stomach contents of over 1,000 dab (Limanda limanda) feeding on invertebrates in the western Baltic Sea. Their results were generally promising, despite a few aberrant parameter estimates. The data were not completely satisfactory because individual prey weights were not measured -- only the mean weight of each prey species in each stomach was available.

Dekker (1983) estimated size preference parameters of North Sea cod (Gadus morhua), following Andersen's model. Because he didn't know the size-spectrum of food available to cod, the author assumed available food was constant over logarithmic size classes. Dekker's study showed that estimating the parameters of Andersen's model is feasible and pointed out the importance of knowing the distribution of available prey.

Ursin and Arntz (1985a) found that the size-preference function of whiting (Merlangius merlangus) was lognormal for whiting feeding on fish but not invertebrates. In a companion paper, re-evaluating the

stomach contents of dab, Ursin and Arntz (1985b) distinguished three different feeding strategies. Food selection was strongly size dependent for some prey species, weakly size dependent for others, and size indiscriminant for a third group. One weakness in these two studies is that the authors only considered size selection, ignoring the interaction between species selection and size selection. Secondly, because they only had mean prey weights instead of individual weights, the authors were not able to characterize the prey size distributions very well. Finally, by lumping data from all seasons together, the authors ignored seasonal changes in prey size distributions. Such seasonal changes could be responsible for the bimodal size-selection curves they observed.

In my study, data were collected with the aim of testing Andersen's model. Yellowtail flounder are primarily benthivores, so a high degree of overlap exists between stomach contents and benthic grab samples. The number and weight of each prey species was measured in both sample types. In addition, individual size distributions of important prey species were measured.

MATERIALS AND METHODS

Fish stomachs were collected on a quarterly basis from Summer 1982 to Spring 1983, on cruises conducted by the NEFC. I participated on two of these four cruises: on the R/V Gloria Michelle in August 1982 and on the Polish R/V Wieczno in February 1983. Stomach collection coincided as closely as possible to the dates and locations of the four benthic monitoring cruises conducted from July 1982 to May 1983. I chose GBMP Stations 5, 10 and 13 (Fig 1-1) for fish stomach analysis because the macrofaunal assemblages differ significantly among these sites. At Stations 10 and 13 trawling was conducted in a 6.5 km square centered at the station coordinates (e.g. Fig. 2-2). At Station 5, to avoid disturbing the site-specific stations, trawling was conducted in the two rectangles shown in Fig 1-2.

An otter trawl, towed at three-hour intervals, usually over a 24-hour period at each station, collected the fish samples. Tow duration was generally 30 min at 3.0 to 3.5 knots. The net was a No. 35 bottom trawl with 18 m legs, 18 m ground cables and 545 kg doors. The cod end and latter section of the upper belly were lined with 13 mm mesh to retain small fish. Fish stomachs were excised at sea, preserved in 10% formalin in sea water and appropriately labelled.

At Battelle Marine Research Laboratory each stomach was cut longitudinally and the entire bolus removed, described according to state of digestion, and wet-weighed to the nearest 1 mg after blotting. Stomach contents were sorted to species and enumerated. Partially digested polychaete fragments were counted if the head was present and an identification could be made. The same protocol was followed for amphipods, except for the species of Unciola. The taxonomic characters

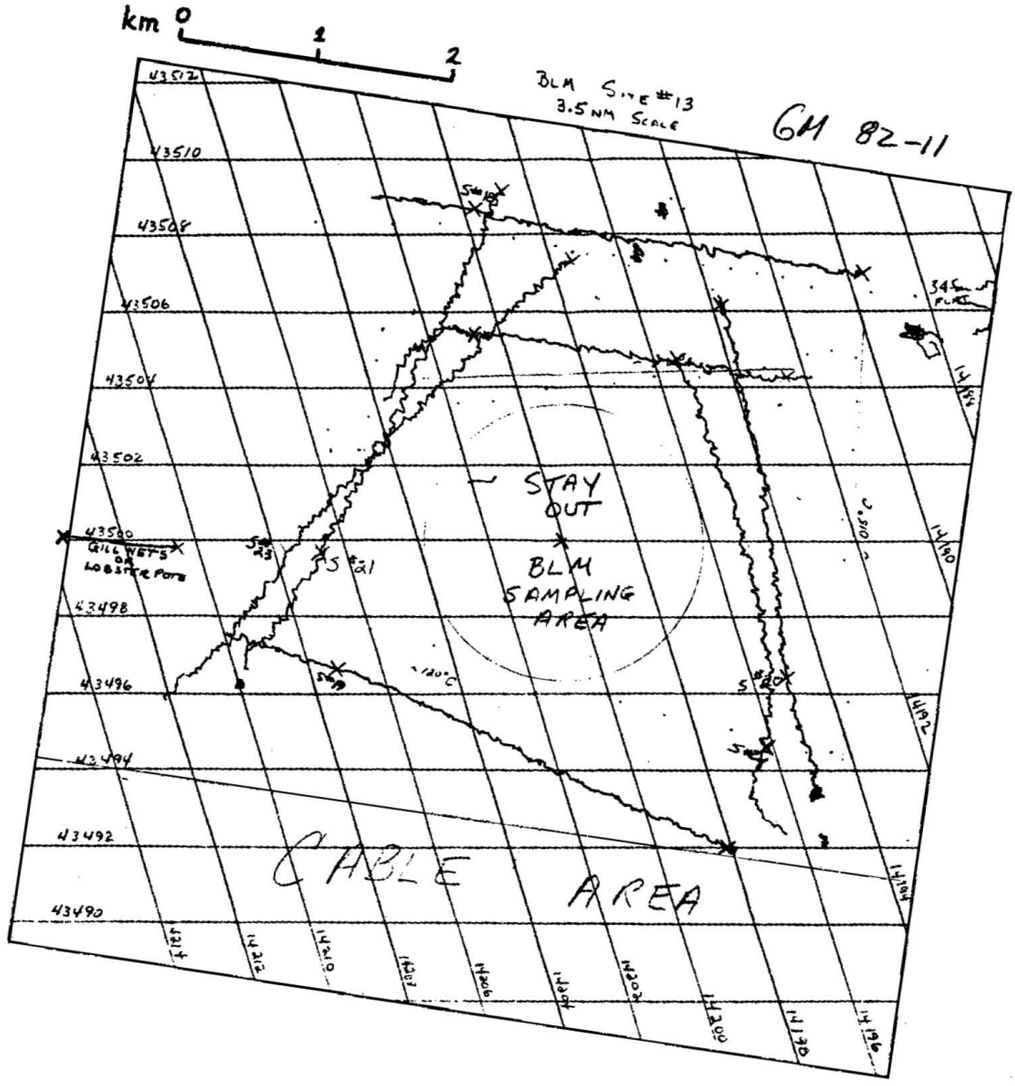


Figure 2-2. Locations of trawls made by RV Gloria Michelle at Station 13 in August 1982. Each wiggly line represents one tow.

needed for species identification in this genus include the third epimeral plate and fifth coxa. The 17% of Unciola prey lacking these characters could not be sorted to species and were recorded as Unciola spp. These individuals were assigned to U. inermis and U. irrorata according to the relative proportions of identifiable individuals of the two species for that station and date. Individuals of each species were weighed together to the nearest 1 mg. Amphipod species were then sent to W.H.O.I. for length-frequency measurements; polychaete species and Echinarachnius parma were retained at Battelle for similar measurements.

The benthic communities at the three sites are described in detail in Battelle and WHOI (1985); species counts and biomass data are filed in the W.H.O.I. VAX 11/780 computer. In addition to the amphipod size-frequency measurements described in Chapter One of this thesis, size measurements were made of 19 polychaete and one echinoderm species (Chapters 7 and 8 in Battelle and WHOI 1985). Only two of the 19 polychaete species were also measured in the fish stomach samples.

Of the site-specific stations, Stations 5-1, 5-18, and 5-28 were the only three that were continuously sampled during the year the fish stomachs were collected. The other site-specific stations were not sampled in February 1983 because of bad weather. Since fish stomachs were collected in the area lying between Stations 5-1 and 5-28, I combined the benthic data from these two stations to calculate food selection.

To investigate the importance of size selection, size measurements were made of six prey species: Unciola inermis and Ericthonius fasciatus from stomachs collected at Station 5, Echinarachnius parma from stomachs at Station 10, and Ampelisca agassizi, Chone infundibuliformis and Levinsenia gracilis at Station 13. These prey species were measured in

the same manner as those from the benthic grab samples (Battelle and WHOI, Chpts. 7 and 8).

Prey selection may vary, not only among fish of different lengths, but also because of behavioral differences among fish. To minimize this potential source of variation, at least for amphipod prey, I examined all stomachs of 31 to 35 cm long flounder for size selection. This was the most abundant flounder size class at all seasons (see Fig. 2-3). I subsampled, with a plankton splitter, stomachs containing large numbers of amphipods such that about 200 prey of each species were measured from each season.

Food selection indices were calculated to compare the species composition of the stomach contents to that of the benthic macrofauna. I modified Andersen's (1982) feeding model to accommodate my data. Andersen's model is based on the assumption that the weight of prey species i, size class j in the diet (S_{ij}), relative to the entire stomach contents (S), is proportional to the availability (Φ_{ij}) relative to the total available food (Φ):

$$S_{ij}/S = \Phi_{ij}/\Phi \quad . \tag{2.3}$$

Although stomach-contents data may be biased by differential prey digestion rates, in the absence of prey-specific digestion rates I assumed the stomach contents accurately reflect the diet.

Available food (Φ_{ij}) is defined as biomass (B_{ij}) weighted by the suitability coeffient (G_{ij}):

$$\Phi_{ij} = B_{ij}G_{ij} \quad . \tag{2.4}$$

Substituting Eq. 2.4 into Eq. 2.3:

$$S_{ij}/S = B_{ij}G_{ij}/\sum_k \sum_m (B_{km}G_{km}) \quad . \tag{2.5}$$

Multiplication of all G terms by the same constant would not change Eq. 2.5. Thus, without changing the biological properties of G, I can add the constraint:

$$\sum\sum_{km} G_{km} = 1.0 \quad . \tag{2.6}$$

Solving for G_{ij} in Eq. 2.5, and using the identity in Eq. 2.6, Beyer and Sparre (1980) obtained:

$$G_{ij} = (S_{ij}/B_{ij}) / \sum\sum_{km} (S_{km}/B_{km}) \quad . \tag{2.7}$$

If prey are classified by species and size, in the diet and in the environment, an array of G_{ij} values can be calculated.

The suitability coeffiecient (G_{ij}) is the product of a species coefficient (ρ_i) and a size-preference coefficient (g_{ij}):

$$G_{ij} = \rho_i g_{ij} \quad . \tag{2.8}$$

Andersen (1982) hypothesized that g_{ij} is a lognormal function of the predator-to-prey weight ratio (W/w):

$$g_{ij} = \exp[-(\log(W/w_j) - \eta_i)^2/2\sigma_i^2] \quad , \tag{2.9}$$

where η_i is the logarithm of the preferred or optimum predator-to-prey

weight ratio, and the variance σ_i^2 measures the breadth of size selection. Taking logarithms of Eq. 2.9:

$$\ln(g_{ij}) = -(\log(W/w_j)-\eta_i)^2/2\,\sigma_i^2, \qquad (2.10)$$

gives a quadratic function of $\log(W/w_j)$ that can be fit by least squares to the observed series of g_{ij} values.

The suitability coefficient is equally amenable to the situation in which prey species are counted instead of weighed. If NS_{ij} and NB_{ij} are the numbers of prey species i, size class j in the fish stomachs and grab samples respectively, then:

$$S_{ij} = NS_{ij}w_j \quad \text{and} \qquad (2.11a)$$

$$B_{ij} = NB_{ij}w_j \quad . \qquad (2.11b)$$

Substituting these expressions back into Eq. 2.7:

$$G_{ij} = (NS_{ij}w_j/NB_{ij}w_j)/\sum_{km}\sum (NS_{km}w_m/NB_{km}w_m) \quad . \qquad (2.12)$$

All the weight (w) terms cancel, leaving:

$$G_{ij} = (NS_{ij}/NB_{ij})/\sum_{km}\sum (NS_{km}/NB_{km}) \quad . \qquad (2.13)$$

Provided the prey are counted and weighed accurately, the suitability coefficient should be identical whether calculated on the basis of weights or numbers.

In electivity notation,

$$r_{ij} = NS_{ij}/NS \quad \text{and} \tag{2.14a}$$

$$p_{ij} = NB_{ij}/NB \quad . \tag{2.14b}$$

By substituting these equalities back into Eq. 2.13,

$$G_{ij} = (r_{ij}/p_{ij}) / \sum_{km}\sum (r_{km}/p_{km}) \tag{2.15}$$
$$= \alpha_{ij}$$

it is easily shown that G_{ij} is exactly equivalent to Chesson's (1978) alpha. This two-dimensional selection index is flexible in that it can accommodate a situation in which not all prey species were measured, or conversely, it can accommodate a situation in which some taxa were measured but unidentified.

In this study I calculated α indices, using Eq. 2.15, on the basis of prey numbers rather than weights. Although biomass is ultimately more important to the predator, I decided, for three reasons, that prey numbers were more reliable. Firstly, the biomass data are unreliable because they are based on preserved, wet weights and the fish-stomach material was semi-digested. Secondly, the benthic biomass data are dominated by a few large animals with hard skeletons such as Arctica islandica and Echinarachnius parma. These heavy animals would bias the selection indices of all other prey species. Finally, to partition the biomass data by size, I would have to convert the size-frequency distributions from numbers to weights in each size class; this would introduce an extra step in the analysis.

NS_{ij} is the number of species i, size class j in the stomach contents. For those prey species not measured I have only NS_i. For prey species that were measured, I used the length-frequency

distributions to partition the total numbers into size classes. If frs_{ij} is the relative frequency of species i, size class j, then:

$$NS_{ij} = NS_i frs_{ij} \quad . \tag{2.16}$$

The size-frequency distributions measured from stomach contents should not be biased by partial digestion because they are based on length measurements that are exactly equivalent for ingested and noningested prey.

NS_i values can be calculated for individual fish stomachs, for groups of fish in a given predator size class or for the entire sample from a given station and date. The size-frequency distributions cannot be calculated for individual fish stomachs because each fish stomach did not contain enough prey to construct a representative distribution. I measured amphipods only from fish in the 31 to 35 cm length class.

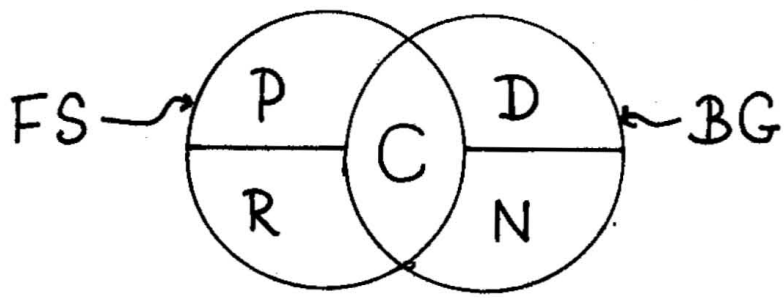
NB_{ij} is the corresponding number of species i, size class j in benthic grab samples. Again, for those prey species not measured, I have only NB_i. For prey species that were measured, I used the length-frequency distributions to partition the total numbers into size classes. If frb_{ij} is the relative frequency of species i, size class j:

$$NB_{ij} = NB_i frb_{ij} \quad . \tag{2.17}$$

Values of NB_i can be calculated for individual replicates or for the sum of all replicates. Size-frequency distributions were not obtained for each benthic replicate but I have assumed the distributions I did obtain represent each replicate in the sample (see Chapter One).

In the first instance, I calculated NS_i and NB_i by summing over all fish stomachs and all benthic replicates from a given station and date, respectively. For Eq. 2.15 to remain valid, it must be assumed that those species not measured are neutrally selected for size.

Fish stomachs and benthic grabs are obviously different types of samplers; the important question is, to what extent do they sample the same populations? The sets of species in the fish stomachs (FS) and in the benthic grabs (BG) do not completely overlap, as shown below:



C is the set of species appearing both in the diet and in the environment. C should be as large as possible and in the ideal case it should be a subset of BG. P is the set of pelagic species eaten by the fish but unavailable to the grab sampler. If P is large, selectivity indices for the benthic species (set C) will be biased downwards. R is the set of benthic species that do not appear in grab samples because they are rare or because they avoid the grab. The first case is true positive selection by fish; in the second case electivity would be overestimated. D is the set of benthic species unavailable to fish, for example because they burrow deeply. If D is large, selectivity for species in set C will be artificially high. N is the set of species available to the fish but truly selected against, for example because they are the wrong size.

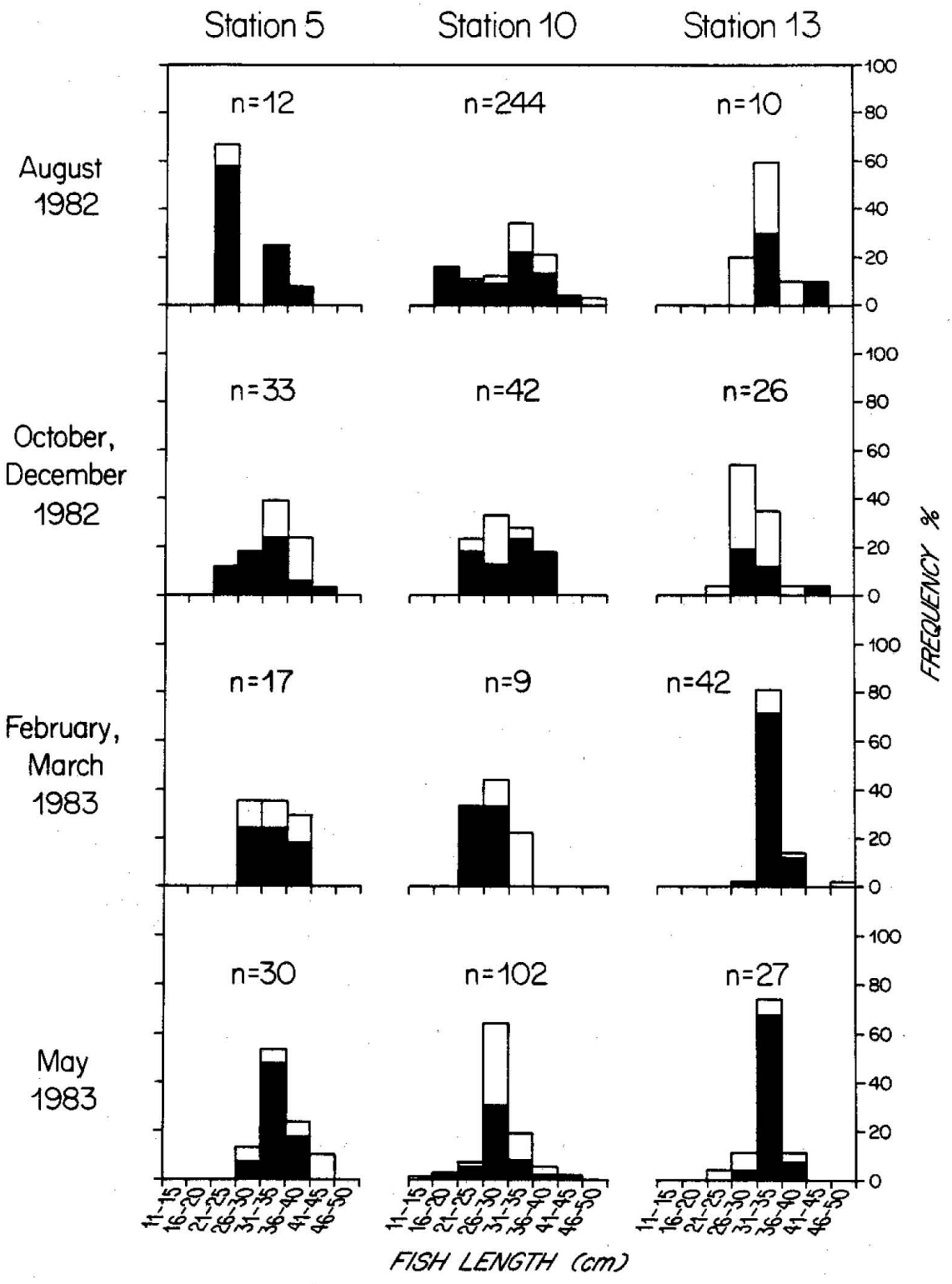


Figure 2-3. Length distributions of yellowtail flounder collected for stomach analysis. Solid bars represent full stomachs; empty bars, empty stomachs.

RESULTS

The numbers of fish stomachs collected are listed, by species, station and season in Table 2-1. (Fish species that are primarily pelagic feeders are excluded from this list.) From this assemblage of demersal fish, I chose yellowtail flounder for stomach analysis because it is relatively abundant, feeds almost entirely on benthic macrofauna and is a commercially important species. In this study, a total of 594 yellowtail flounder stomachs were examined. The length distributions of these fish are plotted in Fig. 2-3. The majority of the yellowtail flounder were between 26 and 35 cm long, which corresponds to an age of three years (Lux and Livingston 1982). Because of the small sample sizes and because most of the flounder occurred in only two of the size classes, I was unable to examine the potential effect of predator length on diet composition.

The stomach contents of these fish are tabulated, by numbers and by weight, in Appendix B. At each station and date, a few prey species constituted the bulk of the yellowtail flounder diet. To illustrate the dominant prey species (Figs. 2-4 and 2-5) I summed the stomach contents over the four seasons. Figure 2-4 shows the five most numerous prey species of yellowtail flounder at each station. These top five prey species accounted for 96%, 70% and 89% of the total identifiable prey at Stations 5, 10 and 13, respectively. Figure 2-5 shows the top five prey species at each station on a weight basis. These species (which are slightly different from those in Fig. 2-4) accounted for 83%, 82%, and 80% of the total weight of identifiable stomach contents at Stations 5, 10 and 13, respectively.

Table 2-1. Numbers of stomachs collected from benthic-feeding fish.

Fish Species	Date and Station: August 1982 5	August 1982 10	August 1982 13	Oct., Dec. 1982 5	Oct., Dec. 1982 10	Oct., Dec. 1982 13	Feb.-March 1983 5	Feb.-March 1983 10	Feb.-March 1983 13	May 1983 5	May 1983 10	May 1983 13	Total
Winter skate	-	-	-	5	58	26	1	26	1	1	92	-	210
Little skate	38	48	3	55	123	41	133	85	48	340	247	21	1182
Red hake	226	82	196	78	1	42	3	3	31	15	1	137	815
Haddock	-	-	-	1	-	-	-	6	1	5	22	1	36
Ocean pout	-	-	3	-	-	-	4	-	41	56	6	6	116
Yellowtail flounder	12	244	10	33	42	26	17	9	42	30	102	27	594
Witch flounder	1	-	66	-	-	-	-	-	3	2	-	14	86
American plaice	-	-	-	-	-	-	-	1	-	-	-	1	2
Gulf Stream flounder	3	-	1	14	11	24	8	-	3	73	13	6	156
Winter flounder	-	-	1	-	-	3	-	-	-	-	-	-	4
Longhorn sculpin	3	4	-	25	6	-	2	-	5	5	39	-	89
Northern sea robin	-	-	-	-	-	10	3	-	1	1	-	1	16

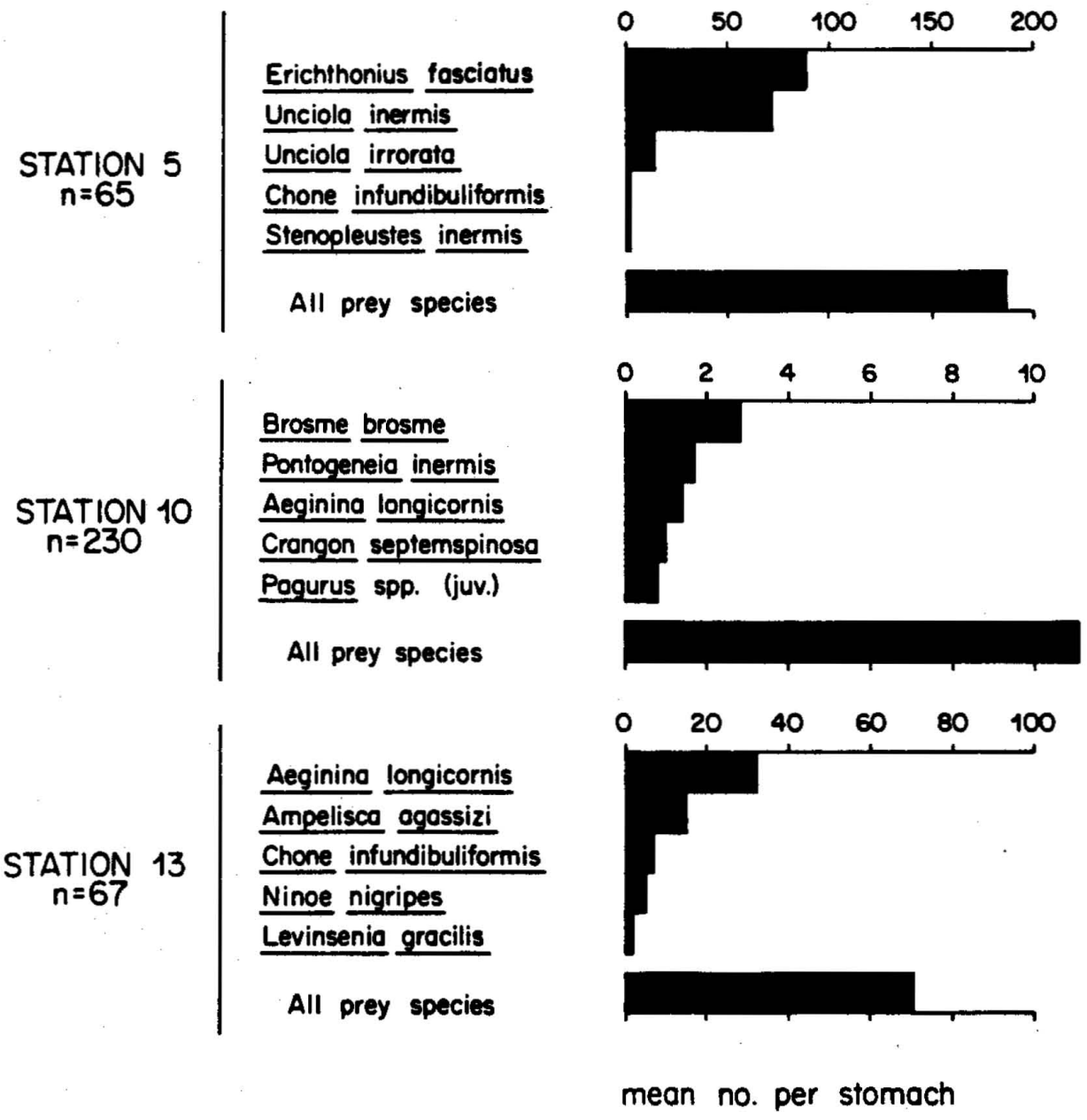


Figure 2-4. Five most numerous prey species of yellowtail flounder at Stations 5, 10 and 13. Data are weighted means of four (quarterly) collecting cruises.

At Station 5 the diet was dominated by tubicolous amphipods and polychaetes. Lumbrineris fragilis was important on a weight basis although only eight of these large worms were eaten. Out of 64 prey species, 52 were also collected in benthic grab samples (set C), three were pelagic (set P) and nine, although benthic were not found in the grab samples (set R). The 12 species in sets R and P constituted an insignificant proportion of the total diet (see Appendix B). Pelagic prey were more important at Station 10 where the diet was dominated by fish larvae, amphipods, shrimps and crabs. Large benthic animals, such as Cerianthus borealis, Echinarachnius parma and L. fragilis, constituted much of the biomass. Of 50 prey species, 31 were in set C, four in set P and 15 in set R. Of the 19 species in sets P and R, nine were important components of the flounder diet (Appendix B). As a result, selectivity at Station 10 for species in set C will be biased downwards. At station 13 the diet was dominated by amphipods numerically, and by polychaetes on a weight basis. Of 56 prey species, 47 were in set C, two in set P and seven in set R. None of the nine species in sets P and R were important components of the diet (Appendix B).

Fish caught at Station 5 had the highest mean number of prey per stomach, followed in turn by those caught at Station 13 and 10. Because the mean weight of stomach contents was only slightly greater at Station 5 (707 mg) than at Station 13 (680 mg) and Station 10 (528 mg), most of the differences in prey number are due to differences in mean prey weight. On the average, flounder ate larger prey at Station 10 (54 mg) than at Station 13 (10 mg) or Station 5 (4 mg).

Seasonal variations in flounder food habits were illustrated in the GBMP Year 2 Report (Battelle and WHOI 1984, Fig. 69). At Station 5 the same prey species dominated the diet at all seasons. In contrast, there

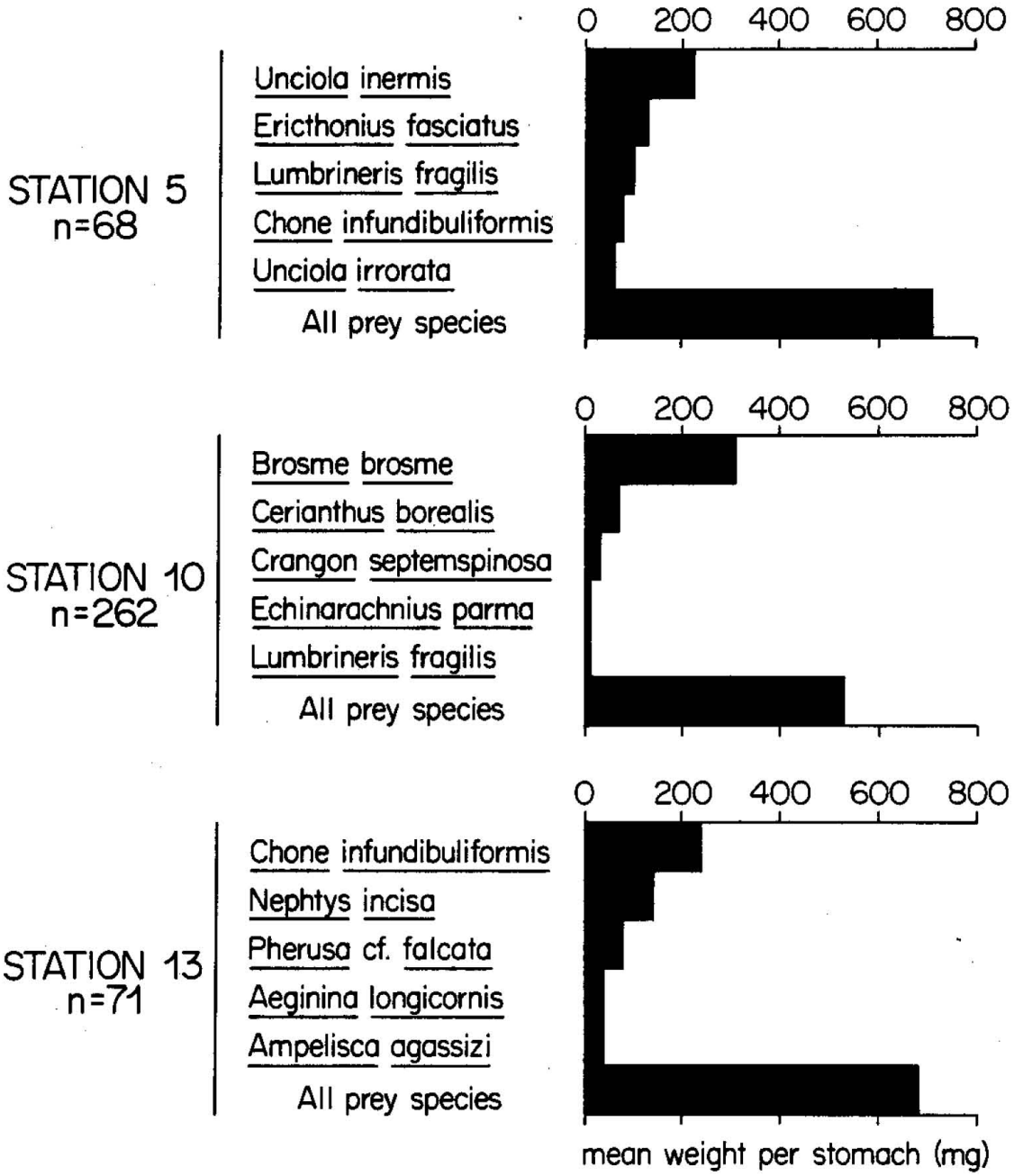


Figure 2-5. Five most important prey species of yellowtail flounder in units of wet weight. Data are weighted means of four (quarterly) collecting cruises.

was considerable seasonal variation in the diet at Station 10. The diet was dominated by larvae of cusk Brosme brosme in August, by the shrimp Crangon septemspinosa in the fall and winter, and by the amphipods Pontogeneia inermis and Aeginina longicornis in May. At Station 13 the diet was relatively constant except for the epifaunal caprellid, A. longicornis, which was eaten in great numbers in winter but much less at other times of the year.

I compared the size-frequency distributions generated from the fish-stomach contents to those from benthic grab samples, with all frequencies expressed as percentages. Due to small numbers of individuals collected, it was not possible to generate size-frequency distributions for all four seasons for all six prey species measured; in some cases it was necessary to pool the size data over four seasons.

I generated length-frequency distributions for Ampelisca agassizi found in flounder stomachs at Station 13 for fall, winter and spring cruises. The small number of stomachs collected during the summer cruise yielded insufficient A. agassizi to measure. Size distributions generated from the grab samples and fish stomachs from May 1983 are compared in Figure 2-6. Flounder neglected the small 3 to 6 mm A. agassizi, selecting the 6 to 8 mm size range.

Length-frequency distributions of Unciola inermis and Ericthonius fasciatus found in flounder stomachs at Station 5 were obtained for all four seasons. I combined the size distributions from grab samples collected at Stations 5-1 and 5-28 by calculating the average percent in each size class, weighted by the densities at each station. The distributions from May 1983 are shown in Figures 2-7 and 2-8. This was a period of recruitment for both U. inermis and E. fasciatus. Again, flounder selected against the juveniles, feeding most heavily on adults.

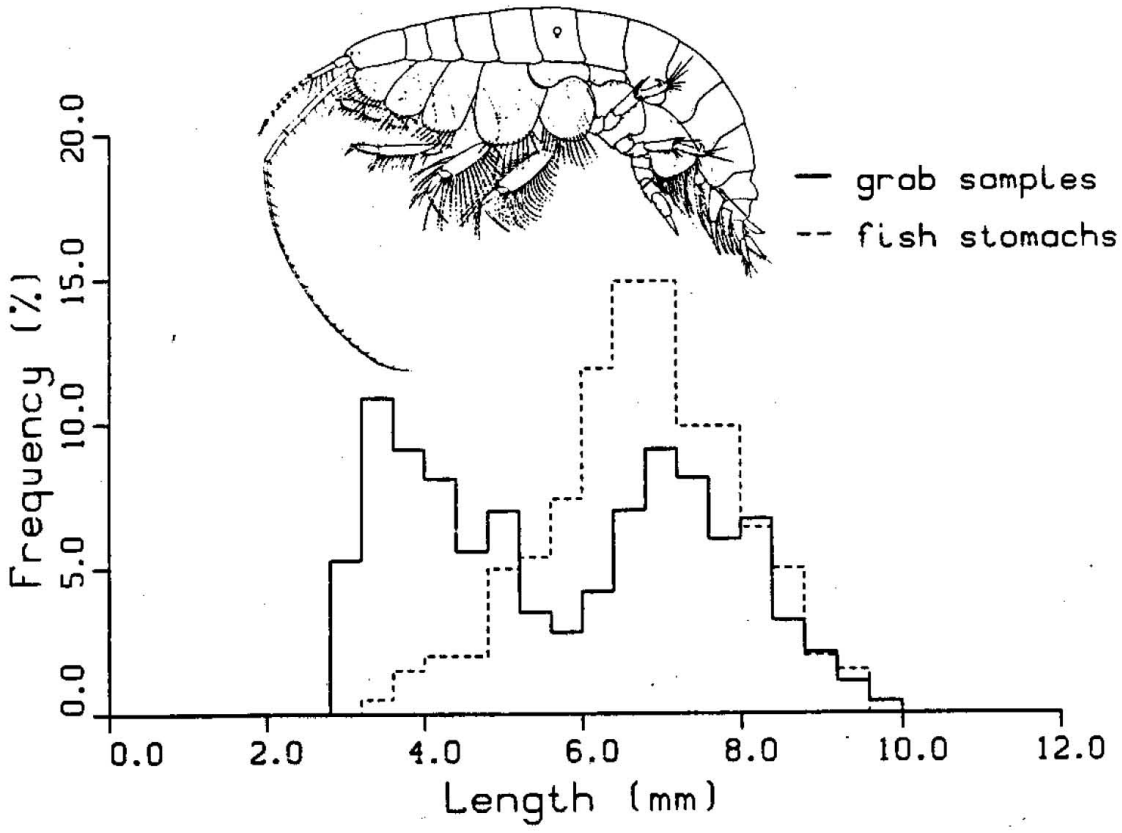


Figure 2-6. Ampelisca agassizi length-frequency distributions at Station 13 in May 1983. The benthic distribution is based on 285 amphipods, which were captured in three grab samples and measured. The ingested distribution is calculated from 214 amphipods removed from 10 yellowtail flounder stomachs and measured.

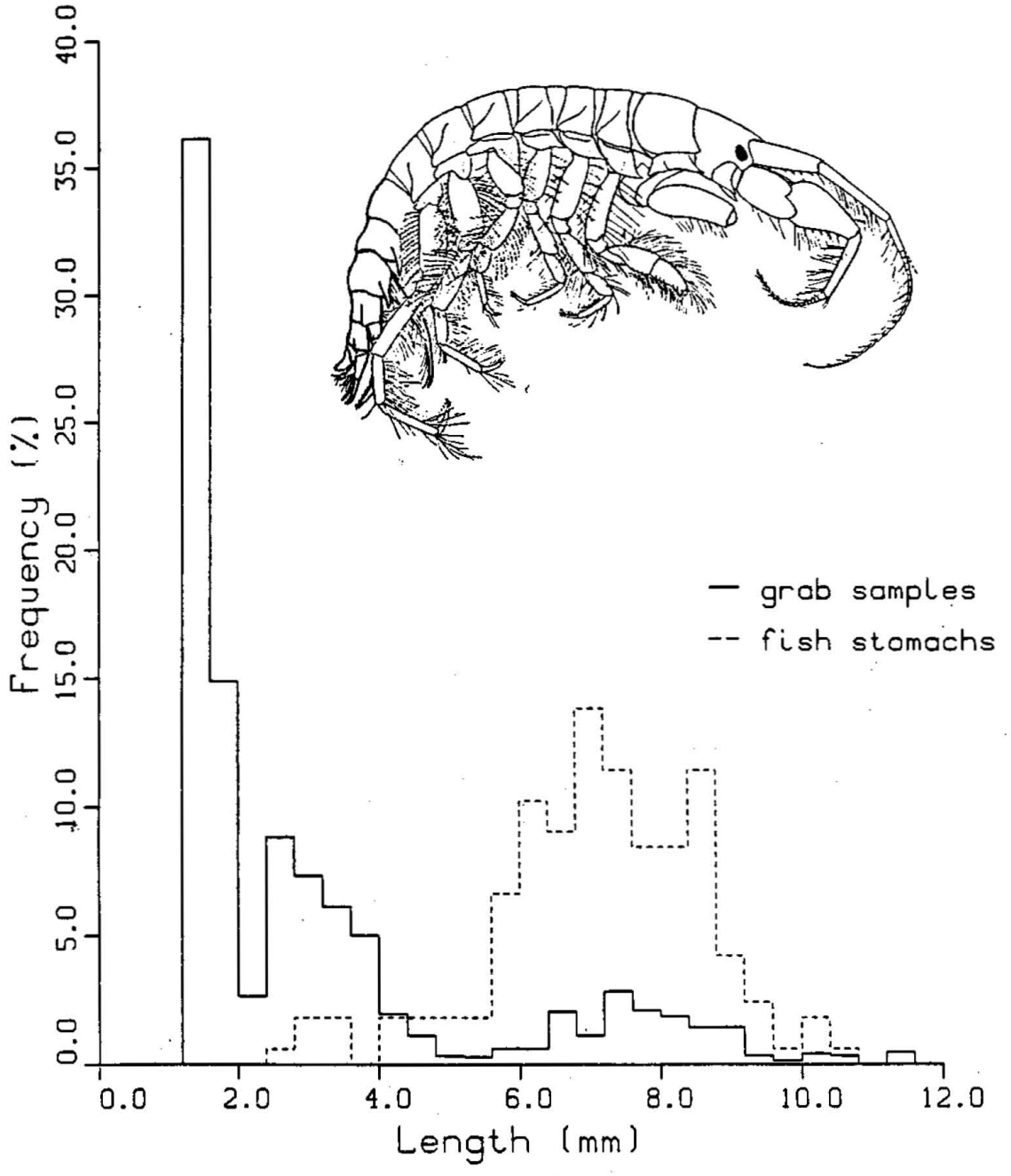


Figure 2-7. Unciola inermis length-frequency distributions at Station 5 in May 1983. The benthic size distribution is a weighted mean of 215 amphipods from Station 5-1 and 220 amphipods from Station 5-28. The ingested distribution is based on 167 amphipods removed from 13 yellowtail flounder stomachs and measured.

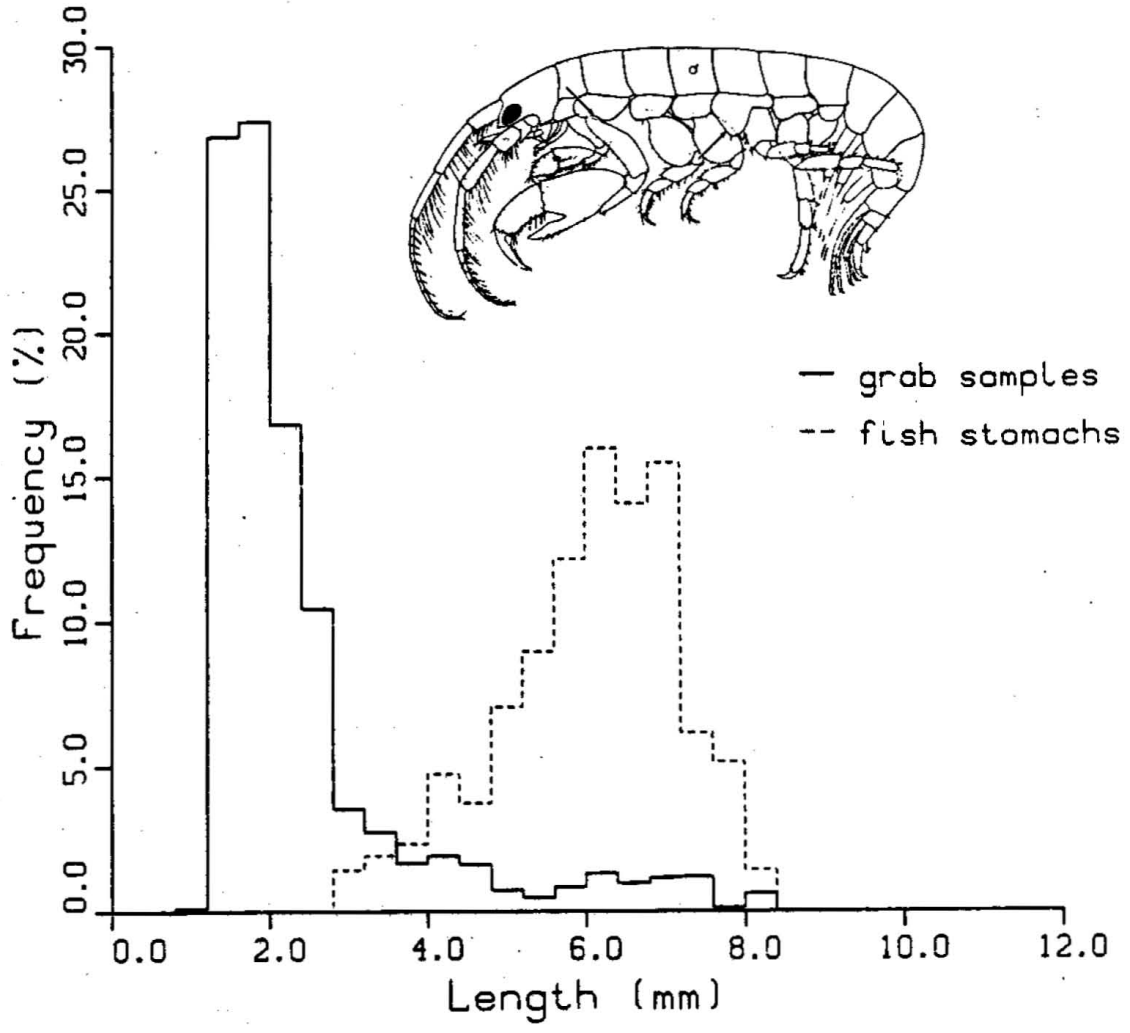


Figure 2-8. Ericthonius fasciatus length-frequency distributions at Station 5 in May 1983. The benthic size distribution is a weighted mean of 157 amphipods from Station 5-1 and 203 amphipods from Station 5-28. The ingested distribution is based on 214 amphipods taken from 10 yellowtail flounder stomachs and measured.

Although Echinarachnius parma is numerically dominant at Station 10, the small number of sand dollars ingested by flounder made it necessary to pool the length-frequency data from all cruises (Fig. 2-9). This is justifiable because, as can be seen from Figure 98 in Collie and Curran (1985), the sand dollars grew only slightly during this period. The benthic grab samples contained juveniles in the 0 to 2 mm size class and larger sand dollars between 10 and 25 m long. Yellowtail flounder, when feeding on sand dollars, almost exclusively chose 6 to 12 mm individuals -- even though this size range was rare in the benthos.

Chone infundibuliformis, in contrast to E. parma, was strongly selected for by flounder despite the former's low abundance in the benthos. Because few of these animals were found in the grab samples, and because the sizes of ingested C. infundibuliformis did not appear to vary with season, I pooled the length-frequency data from all cruises and plotted the distributions in Fig. 2-10. If one allows for the differences in sample sizes, the fish-stomach and grab-sample length-frequency distributions are very similar.

The size measurement used for Levinsenia gracilis was not length but setiger number as estimated using the regression equation in Table 14 of Battelle and WHOI (1985). Although L. gracilis was one of the most numerous species in the grab samples from Station 13, it was not found in flounder stomachs collected in summer and fall 1982. The size-frequency data from February and May 1983 are pooled and plotted in Fig. 2-11. The grab-sample size-frequency data are skewed towards higher setiger numbers. Flounder fed on the same size range as occurred in the benthos, but the fish-stomach size-frequency distribution is more normally distributed and therefore it appears that the fish selected smaller-sized worms.

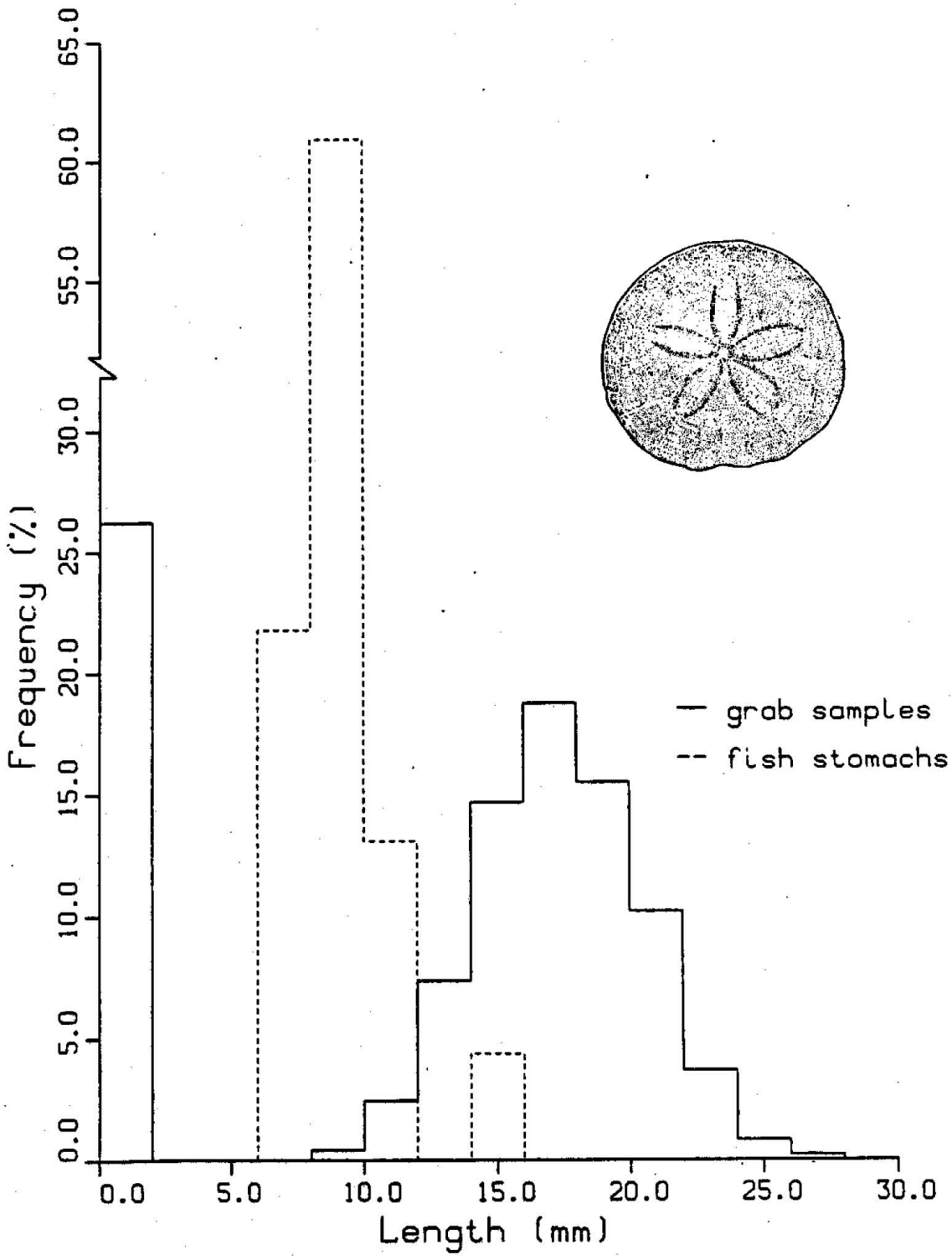


Figure 2-9. Echinarachnius parma length-frequency distributions at Station 10 from July 1982 to May 1983. The benthic distribution is calculated from 492 sand dollars; the ingested distribution is based on 23 sand dollars found in 11 yellowtail flounder stomachs.

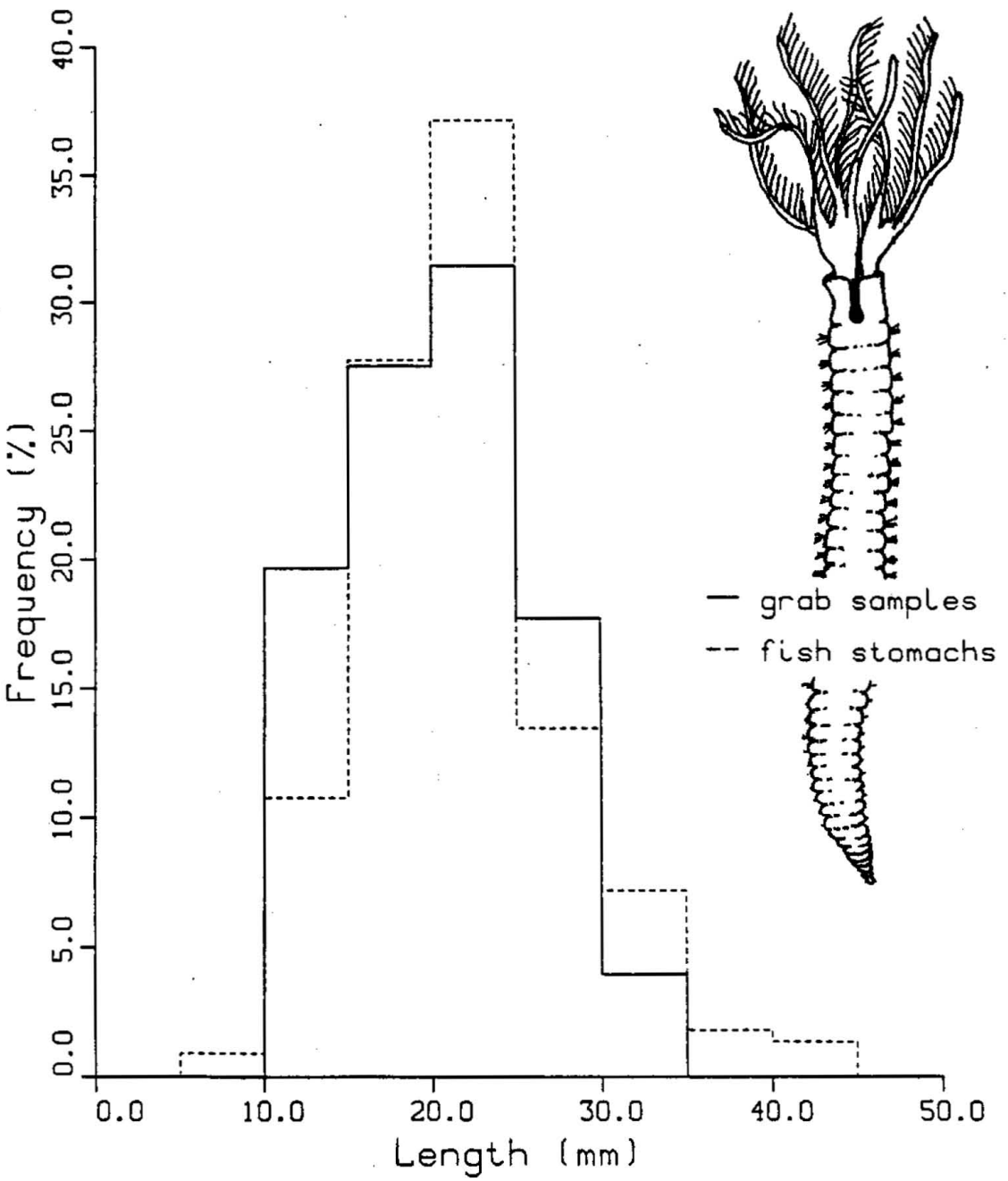


Figure 2-10. Chone infundibuliformis length-frequency distributions at Station 13 from July 1982 to May 1983. The benthic distrbution is based on 51 worms; the ingested distribution is generated from 224 worms found in yellowtail flounder stomachs.

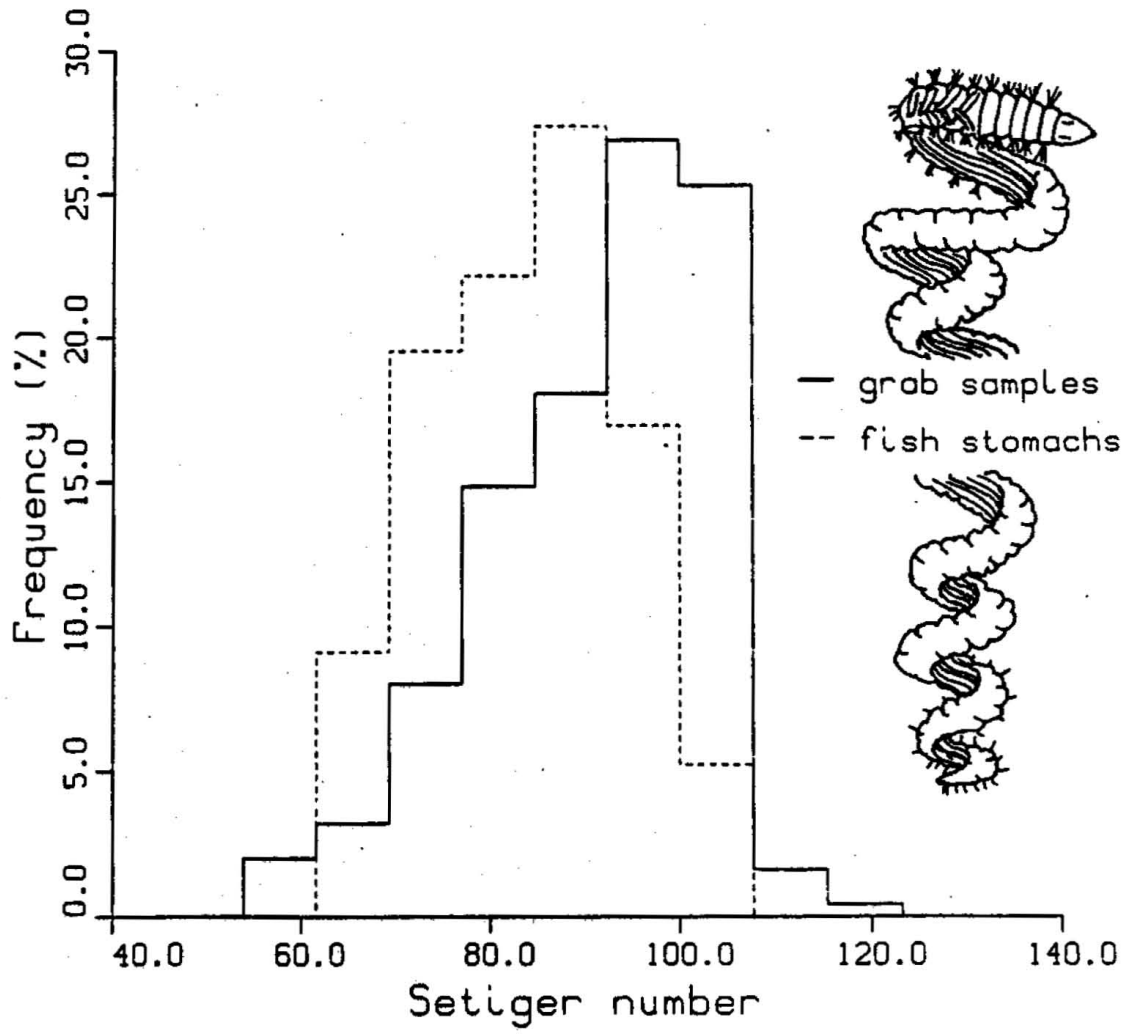


Figure 2-11. Levinsenia gracilis size-frequency distributions at Station 13 from February to May 1983. The benthic distribution is based on 250 worms; the ingested distribution comes from 77 worms eaten by yellowtail flounder.

I calculated α selectivity indices to determine whether changes in prey composition reflect seasonal changes in benthic community composition. Constant α for a given prey species indicates that fish feeding mirrors changes in prey abundance; variable α implies that prey suitability or availability changed during the year.

As a first step in calculating selection indices, I calculated α_i on the basis of prey species only, disregarding the size-frequency data. I did this to compare selectivity among those prey species not measured. Species in sets P and R (pelagic and rare benthic) enter into the calculation of r_i in Eq. 2.15, but α_i is undefined for these species because p_i is zero. Species in groups D and N (benthic species not eaten by fish) enter into the calculation of p_i, but α_i is zero for these species. The α value corresponding to neutral selection is 1/n, where n is the number of prey species. I took n to be the size of set C: those species found both in the fish stomachs and in the grab samples during at least one season. This gives a slightly higher neutral value than if n were the size of set BG: the total number of species in the benthic grab samples.

Seasonal α indices for prey species dominating the diet at Stations 5, 10 and 13 are shown in Figs. 2-12, 2-13 and 2-14, respectively. Pelagic prey were important in the diet at Station 10, but α is undefined for these species. The dashed line in each subplot indicates the α value corresponding to neutral selection. This value is the same for all species and seasons at a given station but varies slightly among stations because the numbers of prey species are different. When examining these plots one must remember that α is based on proportions and the sum of for each season is unity. Therefore, an increase in α for one species results in a decrease for other species and it is impossible to determine

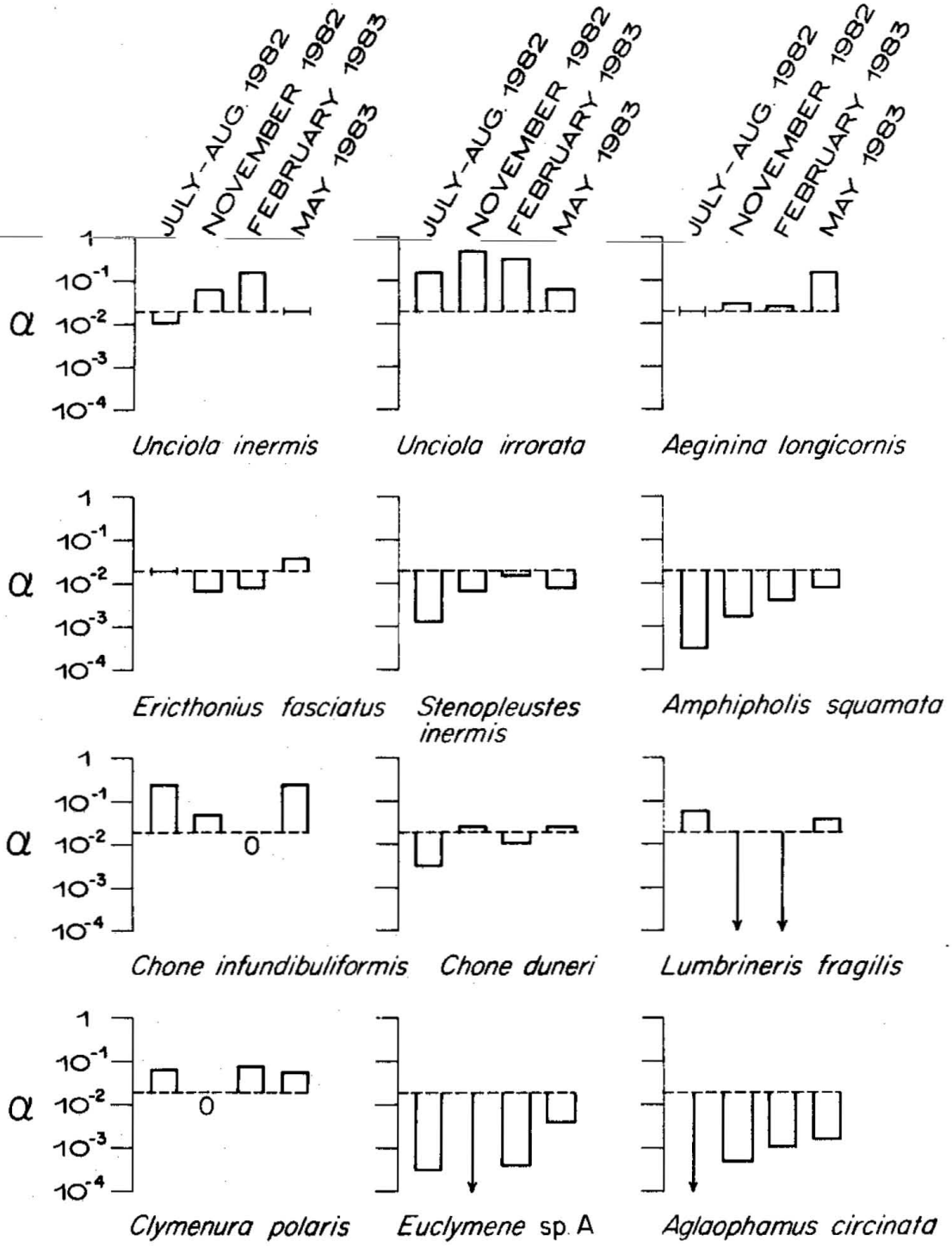


Figure 2-12. Yellowtail flounder selectivity for benthic prey at Station 5. The dashed line in each subplot is the value for neutral selection. Arrows indicate that the prey species was present in benthic grab samples but not eaten by flounder on that date; α is zero in this case. Zeros below the dashed line indicate that the prey species was not found in benthic grab samples on that date; in this case α is undefined.

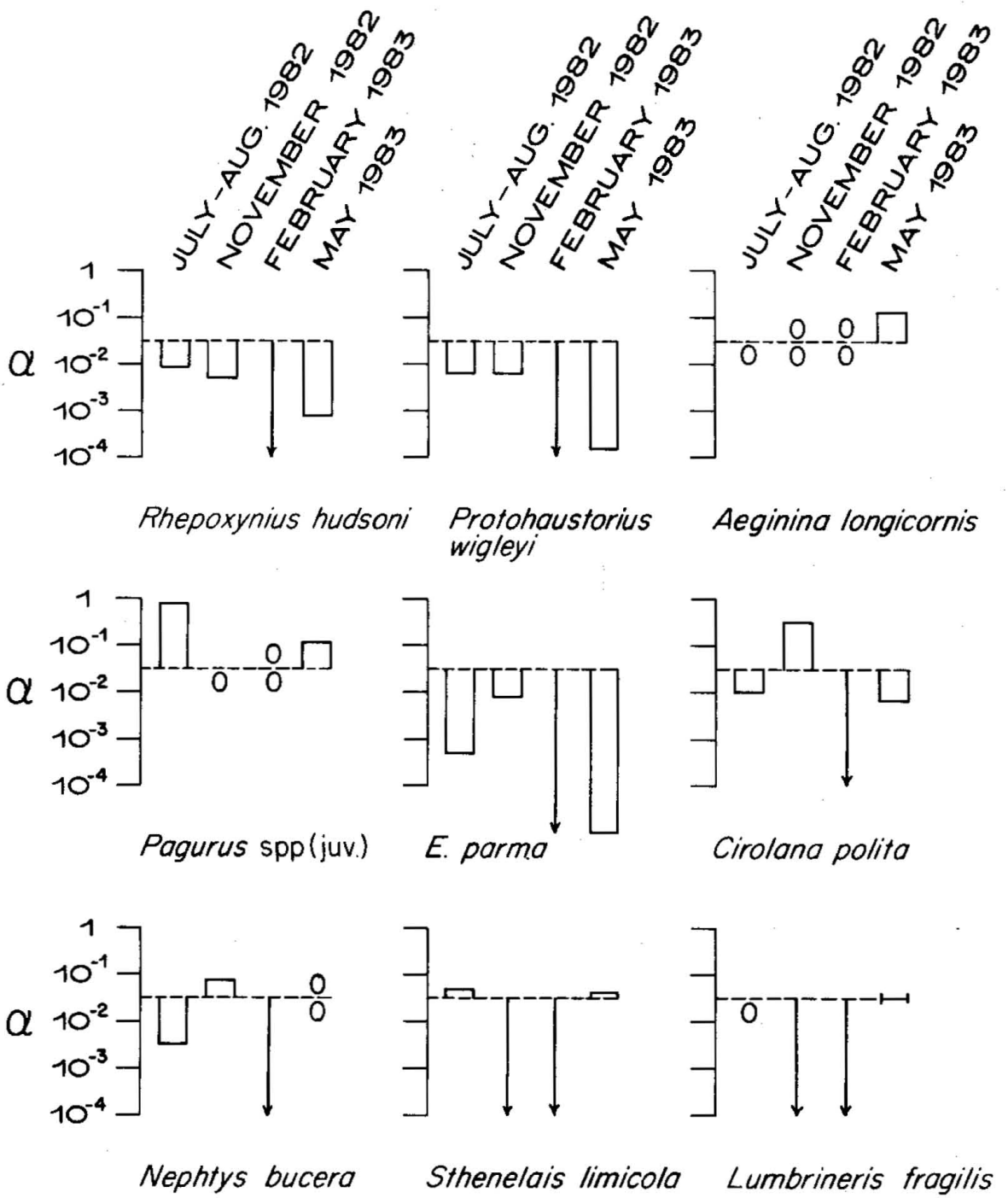


Figure 2-13. Yellowtail flounder selectivity for benthic prey at Station 10. The dashed line in each subplot is the value for neutral selection. Arrows indicate that the prey species was present in benthic grab samples but not eaten by flounder on that date; α is zero in this case. Zeros below the dashed line indicate that the prey species was not found in benthic grab samples on that date; a zero above the dashed line indicates that the prey species was not eaten on that date.

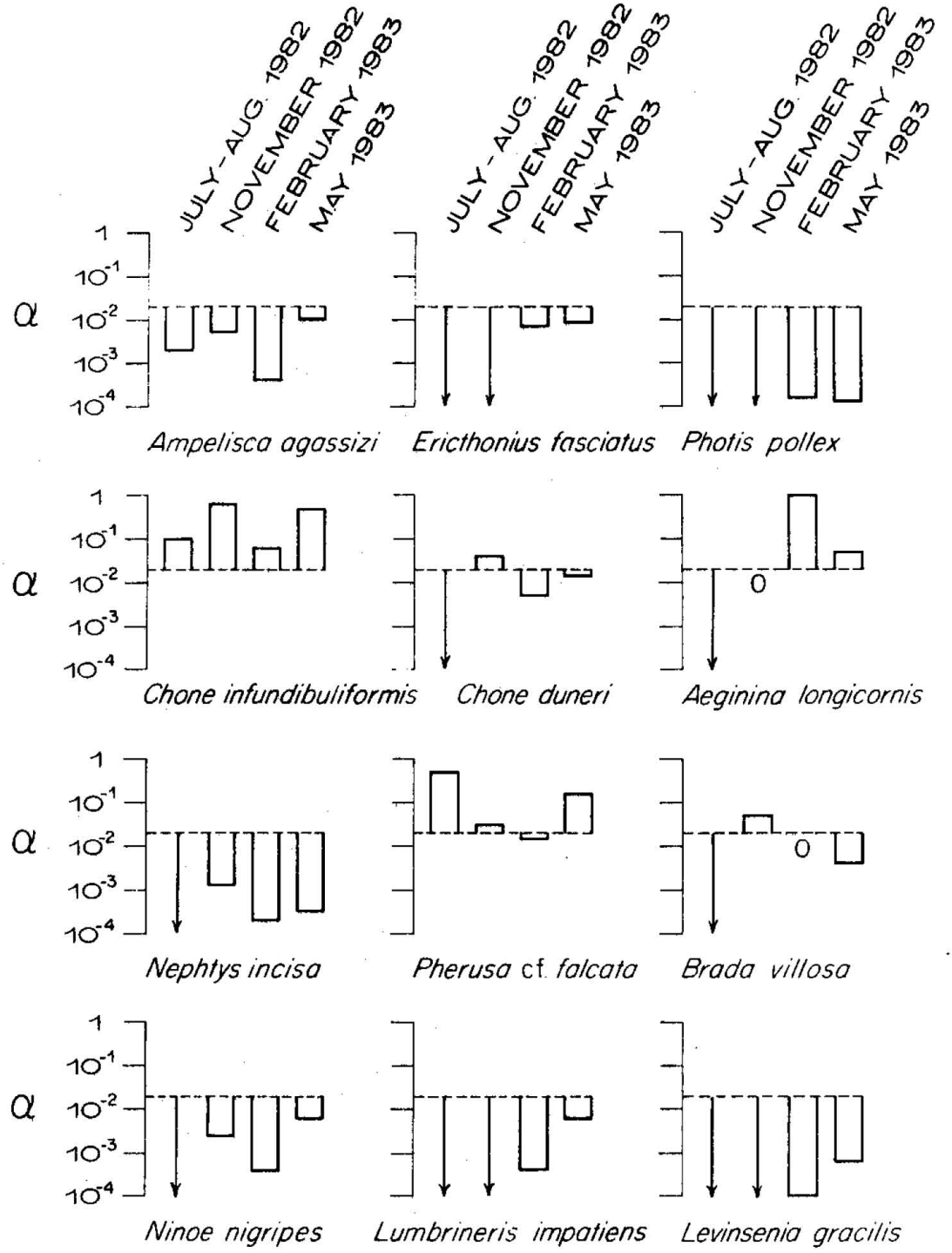


Figure 2-14. Yellowtail flounder selectivity for benthic prey at Station 13. The dashed line in each subplot is the value for neutral selection. Arrows indicate that the prey species was present in benthic grab samples but not eaten by flounder on that date; α is zero in this case. Zeros below the dashed line indicate that the prey species was not found in benthic grab samples on that date; in this case α is undefined.

causality from the index alone.

Of the three stations, seasonal α values were most consistent at Station 5, owing to the high degree of overlap between the contents of the fish stomachs and grab samples there. The α values were most variable at Station 10, due to the predominance of pelagic and rare benthic species in the flounder diet. In July, the high α for Pagurus, which was rare but present in the grab samples, resulted in low values for the remaining species. In May a similarly high α for Pontogeneia inermis (a mainly pelagic amphipod, not shown) diminished α for the remaining species. Seasonal α values were more consistent at Station 13 except in February when Aeginina longicornis dominated the diet but remained rare in the grab samples. The high α value for A. longicornis depressed α for the remaining species.

The yellowtail flounder diet is plastic in that the dominant species vary from station to station. On the other hand selectivity values are consistent for those prey species when eaten at two or more stations. For example, A. longicornis was positively selected at all three stations. Ericthonius fasciatus was almost neutrally selected at Station 5 and slightly negatively selected at Station 13. Chone infundibuliformis was positively selected at Stations 5 and 13; C. duneri was neutral to slightly negatively selected at the same stations. Finally, Lumbrineris fragilis was neutrally selected at Station 10 and slightly positively selected at Station 5.

My second step in calculating selectivity indices was to use the size-frequency distributions of important prey species to partition the prey numbers into size classes. I created new fish-stomach and grab-sample data files, each file consisting of an array of species, some of which are partitioned by size class. Using these new data files, I

Table 2-2. Relationships between length (L) in mm and wet weight (W) in mg for five species as fitted by linear regression to the equation log(W) = a + blog(L). All weights are from live animals except for C. infundibuliformis in which case only preserved worms were available.

Species	n	a	b	r^2
Ampelisca agassizi	87	0.020	2.70	0.97
Unciola inermis	39	0.050	2.48	0.97
Ericthonius fasciatus	86	0.025	2.48	0.98
Chone infundibuliformis	48	0.019	2.59	0.87
Echinarachnius parma	66	0.839	2.38	0.97

calculated α_{ij} values by Eq. 2-15. For the purpose of calculating 1/n (the value corresponding to neutral selection), n is now the total number of prey categories. I converted the length classes, as shown in Figs. 2-6 to 2-10, to weight classes using the length-weight regressions listed in Table 2-2.

In Fig. 2-15, I plotted α_{ij} values of five prey species against prey weight on log-log axes. This plot is a composite, not only of prey species, but also of different stations. The Ericthonius fasciatus and Unciola inermis data are from Station 5, the Echinarachnius parma data, Station 10 and the Ampelisca agassizi and Chone infundibuliformis data, Station 13. Since selectivity values are consistent among stations, as explained above, this among-station comparison of α_{ij} should be valid. For most prey size classes, I could calculate α_{ij} values for all four seasons; Fig. 2-15 shows the mean and range (vertical lines) of α_{ij} values for each species. Again, the dashed line indicates the α_{ij} value corresponding to neutral selection.

Fig. 2-15 compares selectivity among different size classes of different species. Together, the five prey species describe a composite, dome-shaped, size-selection curve. Size selection for the three amphipod species (open symbols) was strongly negative for the smallest (juvenile) size classes and increased with prey size. All sizes of the polychaete, Chone infundibuliformis, were positively, and more or less equally selected. I calculated α_{ij} values for the Levinsenia gracilis size classes shown in Fig. 2-11, but, lacking a conversion from setiger number to wet weight, I could not plot this species' α_{ij} values in Fig. 2-15. All size classes of L. gracilis were negatively selected, as would be expected for such a small worm (mean weight 0.3 mg).

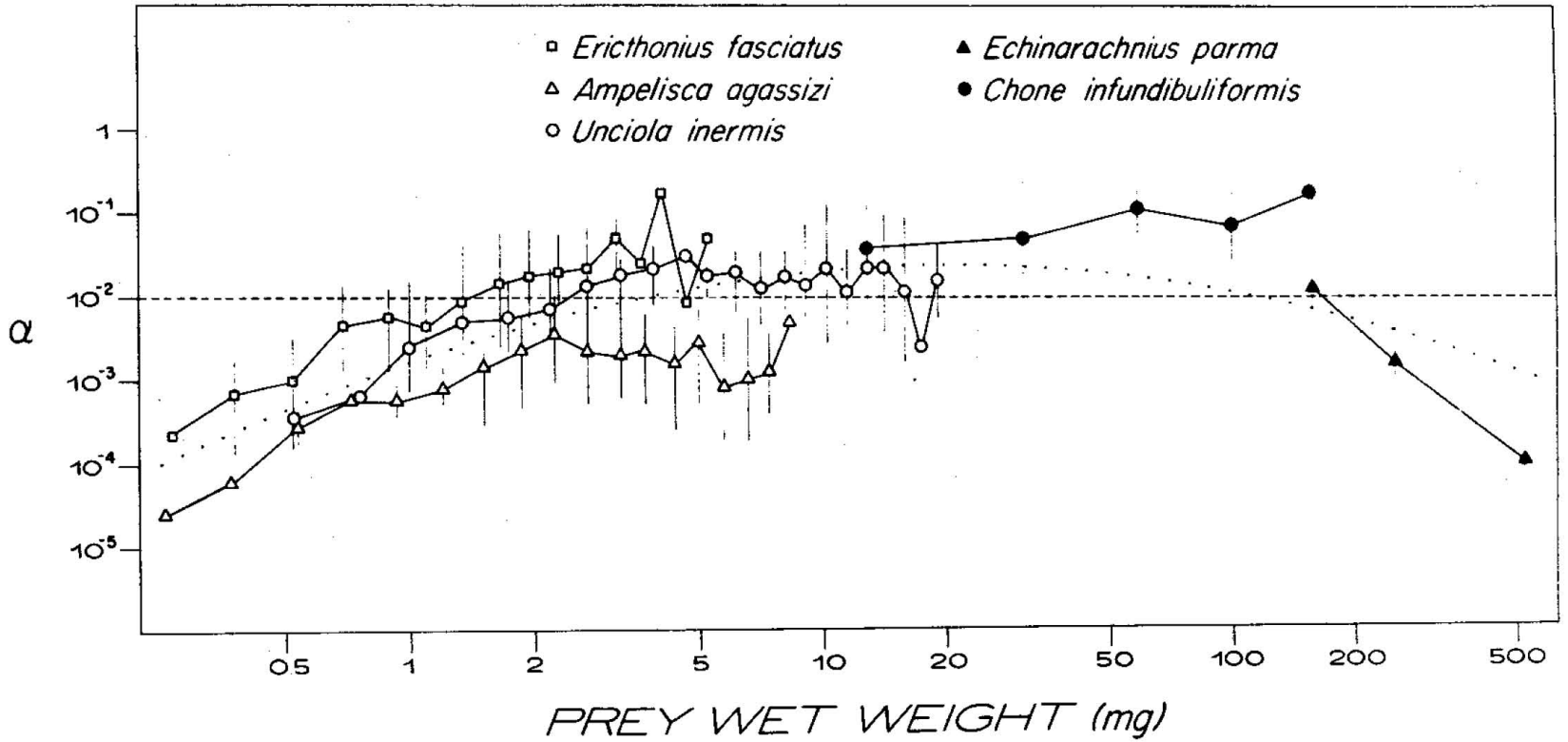


Figure 2-15. Yellowtail flounder size selectivity for five benthic prey species. The symbols indicate the means of four seasonal values and the vertical lines indicate the ranges between minimum and maximum α_{ij} values. The dashed line is the value for neutral selection. The dotted curve is the least-squares fit to Eq. 2-10.

Only three of the Echinarachnius parma size classes plotted in Fig. 2-9 appeared both in the fish stomachs and grab samples; selectivity for all three decreased with prey size. Juvenile sand dollars, weighing approximately 0.5 mg each, were numerous in the grab samples but never eaten by flounder. Intermediate-sized sand dollars, weighing about 40 mg each, were eaten but did not appear in the grab samples. Sand dollars larger than 500 mg each, although abundant at Station 10, were not eaten by flounder. E. parma, by itself, probably describes a dome-shaped size-selection curve but unfortunately, only three of these sizes can be plotted in Fig. 2-15.

In summary, these five prey species define the upper and lower size limits of food acceptable to yellowtail flounder. Prey items between about 2 and 200 mg are positively selected by flounder. In fitting Eq. 2-10 to the observed α_{ij} values, I ignored the species coefficient (ρ_i) because the five prey species define a composite size-selection curve. The least-squares (r^2=0.53) fit to Eq. 2.10 is indicated by the dotted curve in Fig. 2-15 (a lognormal curve is parabolic when plotted on log-log axes). According to this fit, the optimal prey weight is 21.0 mg and the variance (σ^2) of the lognormal size-selection function is 0.34 log(mg).

DISCUSSION

Results of the fish stomach-contents analysis agree with published reports of yellowtail flounder food habits (Langton 1983, Bowman and Michaels 1984) in that arthropods and polychaetes were the major prey groups. Many of the important prey species were the same in my study as those found previously; these include polychaetes (Lumbrineris spp. and Nephtys spp.), amphipods (Unciola spp.), and decapods (Crangon septemspinosa). The two studies cited above were based on the stomach contents of flounder collected over wide geographical areas; not surprisingly, the stomach contents reflected the diversity of benthic communities on which the fish fed. In my study, fish were caught in relatively small areas in which each benthic communities is relatively uniform. Although the flounder diet varied among stations, at each station a few prey species dominated the diet.

Yellowtail flounder feed mainly during the daylight hours (Langton 1983 and Fig. 3-1), from which we infer they are visual predators. The main prey of yellowtail flounder are animals living on or near the sediment surface. The selectivity indices in Figures 2-12 to 2-14 can be interpreted in relation to where the prey species live, how they feed and what size they are. Prey sizes, given in parentheses in the following paragraphs, are mean weights from all fish stomachs at each station and were calculated by dividing the total weight of each species by the number of individuals. Although biased by partial digestion, these weights provide relative sizes for those species not individually measured.

Compared to the electivity indices presented in Collie and Curran (1985, Figs. 104 to 106), fewer species are positively selected according

to the α index. This is because α compares selectivity only among those species occurring both in the diet and in the benthos (set C), while Ivlev's E applies to all species (FS∪GS). As a result, E values tend to the positive and negative extremes, while α values tend to neutral selection.

The numerically dominant prey species at Station 5, Ericthonius fasciatus and Unciola inermis, are both tubicolous amphipods and were approximately neutrally selected (Fig. 2-12). U. irrorata, although much less abundant than U. inermis in the benthos, was more strongly selected for by flounder. U. irrorata usually inhabits tubes constructed by other amphipods or polychaetes, but can build a tube of its own if no others are available (Bousfield 1973). Smith (1950) observed these amphipods swimming or roaming across the bottom, leaving their tubes for considerable lengths of time. U. irrorata (4.5 mg) is more strongly selected than U. inermis (3.3 mg) perhaps because it is more epifaunal in habit or because it is larger.

The caprellid, Aeginina longicornis (3.2 mg), has been collected from sea grass, macroalgae, hydroids and bryozoans (McCain 1968); this epibenthic habit explains its positive selectivity by flounder. The amphipod Stenopleustes inermis is also thought to live on hydroids because other species in its genus have been collected from hydroids (Lincoln 1979) and alcyonarians (Sars 1895). S. inermis is not as strongly selected for by flounder as are the other amphipod species, perhaps because of its smaller size (1.7 mg). The brittle star, Amphipholis squamata (2.7 mg), burrows superficially in sandy substrata (Gosner 1971) and may therefore avoid predation.

The sabellid polychaetes, Chone infundibuliformis and C. duneri feed with tentacles above the surface (Fauchauld and Jumars 1979), exposing

them to predation. C. infundibuliformis (31.8 mg) was selected more stongly than the smaller species, C. duneri (6.5 mg). Most lumbrinerid polychaetes are burrowers (Fauchald and Jumars 1979), which makes them less vulnerable to predation by flounders. Lumbrineris fragilis was positively selected by flounder probably because of its large size (851.0 mg). Most members of the family Maldanidae are tubicolous (Fauchald and Jumars 1979). Of the two maldanids included in Fig. 2-12, the larger, Clymenura polaris (19.5 mg), was selected for and the smaller, Euclymene sp. A (3.3 mg), was selected against. All nephtyids are free-living burrowers (Fauchald and Jumars 1979); this probably explains why Aglaophamus circinata was negatively selected despite its large size (51.4 mg).

At Station 10 (Fig. 2-13) there was less overlap between diet and benthos. Many of the important prey species were pelagic or otherwise rare in the grab samples. The two most abundant amphipod species there, Rhepoxynius hudsoni and Protohaustorius wigleyi, are both burrowers and both were selected against by flounder. The sand dollar, Echinarachnius parma, although it lives on the surface, was negatively selected. The large burrowing worms, Lumbrineris fragilis (180.6 mg) and Nephtys bucera (295.0 mg), were more or less neutrally selected, as were Sthenelais limicola (45.5 mg) and Cirolana polita (41.0 mg).

Station 13 (Fig. 2-14) had the greatest overlap between fish diet and macrobenthos. Ampelisca agassizi, the dominant amphipod species there, builds its tubes verticaly into the substratum and may thus avoid predation. Another amphipod species, Photis pollex, was strongly selected against, probably because of its small size (0.3 mg). The flabellegerid polychaetes, Pherusa cf. falcata (108.9 mg) and Brada villosa (51.2 mg), are surface-dwelling deposit-feeders (Fauchald and

Jumars 1979); together with their large size, this probably explains their positive selection by flounder. The remaining polychaete species are all sub-surface burrowers and were all negatively selected.

Figures 2-6 to and 2-8 showed that predation on amphipods was size dependent. Selectivity indices calculated for each amphipod size class (Fig. 2-15) indicate that size selection was consistent among seasons and among prey species. In general, selectivity was strongly negative for juveniles, increased with prey size, and was more or less constant for adult (larger than 2 mg) amphipods. Several authors have noted that mature amphipods spend more time than do juveniles swimming in the water column (see Chapter One). This could partly explain the higher selectivity values for the larger amphipods, as all three species mature at about 2 mg.

Even when selectivity is standardized for the effect of size, differences are apparent among the amphipod species. In other words, at a given prey weight, Ericthonius faciatus is most highly selected and Ampelisca agassizi the least selected. As I discussed in the Chapter One, this observation can be explained by the species' different life-history strategies. E. faciatus, the most epifaunal in habit, is most vulnerable to predation; Unciola inermis is intermediate in these traits; A. agassizi, the most sedentary, avoids predation by building its tubes into the substratum.

Yellowtail flounder predation on Echinarachnius parma (Fig. 2-9) was strongly size selective. Sand dollars 6 to 12 mm long were selected for while juveniles and individuals larger than 12 mm were selected against. Presumably, no 2 to 6 mm sand dollars were available in the benthos. Due to the relatively small mouth gape of yellowtail flounder, it probably cannot feed on sand dollars larger than 16 mm, tentatively explaining the

negative selectivity values obtained for E. parma in Fig. 2-13. Flounder selected sand dollars within a narrow size range, and most of the sand dollars at Station 10 were either too big or too small. Predation by yellowtail flounder and other fish on the intermediate sizes of E. parma species could explain the absence of such sand dollars in benthic grab samples and why juvenile E. parma did not appear to survive and grow.

There was a very close correspondance between available and ingested prey sizes of Chone infundibuliformis (Fig. 2-10). Fig. 2-15 shows that all size classes were positively selected by flounder, suggesting that C. infundibuliformis is the optimum prey size. Yellowtail flounder appeared to select the smaller sizes of Levinsenia gracilis (Fig. 2-11). This is surprising because L. gracilis is a very small worm species -- smaller than flounder generally choose. Rather than being selected by flounder, it seems probable that L. gracilis was eaten incidentally since it is very numerous at Station 13.

To meaningfully compare size selection among prey species, a common unit of measurement is necessary. If flounder are gape limited, prey width determines what will fit through the mouth. Wet weight is important because it determines the amount of prey biomass eaten; ash-free dry weight is important because it determines the actual food value obtained. By converting prey sizes to wet weights I obtained the continuous size-selection curve given in Fig. 2-15; it suggests that biomass may be an important criterion of size selection.

Selection against juvenile amphipods and sand dollars and against the small worm, Levinsenia gracilis, indicates that there is a minimum suitable prey size. Two factors could define this minimum size threshold. A sensory limit may exist if flounder cannot detect prey below a certain size. Or, foraging for such small prey may be energetically

inefficient. Since sand dollars are hard and approximately round, the width of a sand dollar must be able to pass through the flounder mouth. Therefore the largest sand dollar eaten (16 mm) is probably a good measure of the maximum gape size.

The overall mean weight of yellowtail flounder caught in this study was 312 g (weighted mean calculated from Appendix B) and the optimal prey size was 21 mg. Thus, the predator (W) to prey (w) weight ratio is about 15,000:1 and the logarithm, log(W/w), is 4.2. This ratio is equivalent to η in Eq. 2.9 and is consistent with other authors' findings. Hahm and Langton (1984) calculated a mean log(W/w) value of 4.2 for both yellowtail flounder and witch flounder. Arntz and Ursin (1981) calculated an array of η values for various size classes of dab (Limanda limanda) feeding on nine prey species; the mean η value was 3.6.

Andersen (1982) proposed that size selection is a lognormal function of prey size (Eq. 2-9). According to this arguement, a prey item twice as large as the optimum size should be selected equally to a prey item one half the optimum size. This lognormal function has been successfully fit for whiting eating fish (Ursin and Arntz 1985a) and for dab feeding on fish (Ursin and Arntz 1985b). Hahm and Langton (1984) plotted frequency distributions of log(W/w) for cod, silver hake and yellowtail flounder. Although these frequency distributions are jagged and skewed, it is easy to imagine them fit by normal curves.

In contrast, Zaret (1980) argued that gape-limited predators should prefer the maximum prey size they can swallow, such that the pattern of selectivity should abruptly truncate at the maximum prey size set by morphology. Schmitt and Holbrook (1984b), testing this hypothesis, found that black surfperch and striped surfperch were not gape limited and that size-selection curves were roughly bell shaped. My composite, size-

selection curve (Fig. 2-15) was fit reasonably well by a lognormal curve. Alpha falls off abruptly for large Echinarachnius parma, suggesting a truncated distribution, but the α values have too much scatter to draw a firm conclusion. The upper size limit, imposed by gape limitation, is certainly more rigid than the lower, more flexible size limit imposed by foraging constraints.

I return finally to the question of whether predation patterns are predictable if the abundance, life history and size distributions of prey species are known. Most of the among-species differences in selectivity (Figs. 2-12 to 2-14) can be explained by prey life history and size. Size selection also may account for some of the among-season variability in selectivity. For example, selectivity for Unciola inermis (Fig. 2-12) was lower in the spring and summer when juveniles were abundant (Fig. 1-4) and higher in fall and winter when only the adult sizes, which are preferred by flounder, were present. Similarly, selectivity for Echinarachnius parma (Fig. 2-13) was lowest when the number of juveniles was highest (Collie and Curran 1985, Fig. 98). This explanation of among-season variability, however appealing, is not supported by the other two amphipod species I studied in detail.

Fig. 2-15 showed that size-selection is important but that among-species differences persist even when the data are standardized for size. There was considerable among-season variation in size selectivity for each species. This variation was not random, but rather, all values for a season were higher or lower than the mean. Some of this residual variation, not accounted for by the size-selection index, is due to the fact that the benthic grab did not adequately sample all the species in the fish diet (sets P and R). This was especially true at Station 10 where high α values for Pagurus spp. and Pontogeneia inermis depressed

the α values for the remaining species. Aeginina longicornis had a similar effect at Station 13 in February when it dominated the diet. A. longicornis, residing on hydroids, is very patchily distributed and therefore its abundance is not measured well by a small grab sample.

An alternative explanation is that flounder feeding behavior switches in relation to prey abundance. Selectivity indices assume that prey species are eaten in proportion to their abundance in the environment. However, switching behavior has been observed in several fish species (Murdoch et al. 1975, Love and Ebeling 1978) and it is evidently induced by threshold prey densities (Pyke 1979). My field study was not designed to detect this more complex behavior; a controlled, manipulative experiment would be required to test this hypothesis.

CHAPTER THREE

RATE OF FOOD CONSUMPTION BY YELLOWTAIL FLOUNDER

INTRODUCTION

In this chapter I estimate the rate of food consumption by yellowtail flounder. Chapter Two dealt with the composition of the flounder diet; Chapter Three is on the quantity of food eaten. My main reason for estimating consumption is to be able to compare the rates of food consumption by flounder to production rates of important prey species. From this comparison, one can infer the effect of flounder predation on benthic prey populations. Chapter Three is a synthesis of results presented in Chapters One and Two, new stomach-content data and information from other studies.

To estimate food consumption by fish in the sea, one must know the consumption rate per fish and the density of fish in the sea; each of these is a non-trivial problem in itself. By maintaining fish in aquaria, one can be measure consumption rate directly, but such data may bear little relation to natural feeding rates. Food consumption in the sea must be estimated indirectly, by bioenergetic calculations or from stomach contents. Both approaches have been used to estimate food consumption rates for several important Northwest Atlantic fish species.

According to the bioenergetic approach, consumption is the amount of food a fish requires to satisfy its total metabolic requirements. Grosslein et al. (1980) used this method to estimate annual consumption by six fish species on Georges Bank. Consumption (C), in units of weight, was calculated as:

$$C = (G + S + Q)/a \quad , \tag{3.1}$$

where growth (G), reproduction (S) and respiration (Q) are all functions of weight. The assimilation coefficient (a) was assumed to be 0.8. The consumption to biomass ratio (C/B) of yellowtail flounder ranged from 6.5 for age 1 fish to 3.0 for age 10 fish; the mean C/B over all ages was 4.6 (Grosslein et al. 1980, Tables 16 and 21).

The stomach-content method of estimating consumption rate is based on the amount of food in the stomach and its rate of elimination. Durbin et al. (1983), in reviewing evacuation rate studies, concluded that an exponential model of gastric evacuation provides a good fit to most experimental data. If one assumes that the rate of food intake (F) is constant over some sampling interval and that the hourly rate of gastric evacuation (r) is proportional to the weight of food in the stomach (S), the rate of change in stomach contents can be expressed by the differential equation,

$$dS/dt = F - rS \tag{3.2}$$

(Elliott and Persson 1978). The solution obtained by integrating Eq. 3.2 is,

$$S_t = S_o \exp(-rt) + F(1-\exp(-rt)/r \quad . \tag{3.3}$$

Given the above assumptions, F is the consumption (C) during the interval 0 to t. Rearranging,

$$C = rt(S_t - S_o \exp(-rt))/(1-\exp(-rt)) \quad . \tag{3.4}$$

Eq. 3.4 is useful for estimating consumption from stomachs contents of fish sampled periodically over a time-span of at least 24 hours. These consumption estimates may be biased if the feeding rate is not constant during the sampling interval; Eggers (1977) recommended an interval not longer than three hours.

Eggers (1979) pointed out that a correct solution to Eq. 3.2 is also:

$$rt\bar{S} = C - (S_t - S_o) , \tag{3.5}$$

where $\bar{S}$ is the mean stomach-content weight from time 0 to t. For fish with daily feeding patterns, stomach-contents weight should be nearly equal at a given time on successive days. Daily consumption (C_{24}) is then:

$$C_{24} = 24r\bar{S} . \tag{3.6}$$

Pennington (1981) showed that Eq. 3.5 is an unbiased estimator provided the samples are collected randomly over time. Furthermore, if t is large, the difference, $S_t - S_o$, in Eq. 3.5 is insignificant. Therefore, Eq. 3.6 holds for large t even if feeding is aperiodic.

It is evident from Eq. 3.6 that the food consumption estimate depends directly on the gastric evacuation rate (r). This rate, r, has been determined for several species of marine fish but not for yellowtail flounder. Gastric evacuation rates are affected by temperature, food type, food particle size, meal size and feeding regime (Fange and Grove 1979); of these factors, temperature and food type are the most important. Durbin et al. (1983, Appendix 1) plotted gastric evacuation

rates (r), of marine and freshwater fish, as a function of temperature. The slopes of the relation between log(r) and temperature (T) were similar for different fish species, but the intercept depended on prey type. For several species of marine fish (cod, flounder, menhaden) fed small prey (less than 0.5 mg), the relationship between r (hr^{-1}) and T (^{o}C) was:

$$r = 0.0406\exp(0.111T) \quad . \tag{3.7}$$

Estimates of fish population abundance are required not only for ecological studies, such as this one, but as a basis for fisheries management. Herein is a short review of the large literature on enumerating fish populations, as it pertains to yellowtail flounder abundance on Georges Bank. There are several different methods of enumerating fish, each with strengths and weaknesses. The choice of method depends on the type of fish, its habitat and the eventual use for the data. For many management purposes, overall population size is the most important result; for ecological studies, such as this one, fish abundance per unit area is needed.

Uzman et al. (1977) compared three direct methods for estimating the abundance of megafauna on Georges Bank: manned submersible, towed camera sled and standardized otter trawl. In all three methods, faunal density was calculated by dividing the number of animals in each taxonomic group by the area covered. The submersible and camera sled were more effective than the trawl in enumerating benthic species; the otter trawl yielded the highest estimates for pelagic fish and squid. The main drawbacks to submersible and camera surveys are that it is possible to cover only relatively small areas, and that it is often not possible to identify

animals to the species level. The otter trawl provides specimens for direct examination, but is a relatively inefficient sampler.

Indirect methods of estimating fish abundance include catch-data analysis, tag-recapture studies and acoustic surveys. Time series of fisheries catch data can be used in several different ways (Cushing 1981, Chapter 5) to reconstruct fish population dynamics and thus to estimate population size. By definition, these methods apply only to exploited populations and perform better as the level of exploitation increases. The drawback to using such methods for estimating fish density per unit area is that the population estimates usually apply to a broad geographic region. One must assume that the fish population is uniformly distributed in a specific area and that there is no mixing between populations.

Collie and Sissenwine (1983) developed a method of estimating population size based on commercial catch data and standardized, otter-trawl, survey data. In essence, this method uses commercial catch data to standardize the survey's relative abundance data. The method also accounts for the error inherent in measuring relative abundance. We estimated the abundance of yellowtail flounder on Georges Bank and in Southern New England as examples of how the method works.

Consumption rate per fish has been calculated for several North Atlantic fish species; these studies are summarized in Table 3-1. When the consumption rates are expressed as percent body weight per day, it is evident that smaller fish eat proportionately more than larger fish of the same species. The consumption rates vary from 0.8% for 60-cm-long cod to 3.2% for silver hake less than 20 cm long. The results agree remarkably well, despite the different methods used by different authors.

Grosslein et al. (1980) calculated consumption per unit area by multiplying their C/B by the fish population biomass (as estimated from

Table 3-1. Consumption rates of seven North Atlantic fish species.

Species	Length (cm)	Location	Method	Consumption Rate % body wt. day^{-1}	Reference
Herring	all	Georges Bank	bioenergetics	1.26	Grosslein et al. (1980)
Mackerel	all	Georges Bank	bioenergetics	1.18	Grosslein et al. (1980)
Silver hake	all	Georges Bank	bioenergetics	1.34	Grosslein et al. (1980)
	<20 cm	Northwest Atlantic	stomach contents	2.9-3.2	Durbin et al. (1983)
	>20 cm	" "	" "	0.8-2.2	" " " "
Cod	40 cm	North Sea	stomach contents	1.3	Daan (1973)
	60 cm	" "	" "	0.8	" "
	40 cm	" "	bioenergetics	1.14	Jones (1978)
	" "	" "	stomach contents	1.3-1.7	" "
	60 cm	" "	bioenergetics	0.8-1.2	" "
	" "	" "	stomach contents	1.4-1.9	" "
	all	Georges Bank	bioenergetics	0.9	Grosslein et al. (1980)
	>30 cm	Northwest Atlantic	stomach contents	0.9-1.5	Durbin et al. (1982)
Haddock	50 cm	North Sea	bioenergetics	1.51	Jones (1978)
	" "	" "	stomach contents	1.19	" "
	all	Georges Bank	bioenergetics	0.88	Grosslein et al. (1980)
Yellowtail flounder	all	Georges Bank	bioenergetics	1.26	Grosslein et al. (1980)
	"	" "	stomach contents	0.2-1.7	This study
Winter flounder	?	Laboratory	direct observation	2	Tyler and Dunn (1976)
	10-40 cm	"	" "	1.8-2.4	Huebner and Langton (1982)
	50.5 cm	Georges Bank	?	1.3-1.5	

catch data) and dividing the area inhabited by the population into the resultant total consumption. I converted their results from kilocalories to grams wet weight, assuming 1 kcal is equivalent to 2 g (Crisp 1984). Therefore, consumption by yellowtail flounder was 5.8 g m^{-2} yr^{-1} from 1964 to 1966 and 4.4 g m^{-2} yr^{-1} from 1973 to 1975. Consumption by all fish species on Georges Bank, during the same periods, was 384.1 and 222.7 g m^{-2}, respectively.

Peterson (1979) discussed the various methods used to determine whether predators regulate the abundance of benthic macrofauna. One way is to undertake manipulative experiments which usually involve excluding and/or including predators in mesh cages fixed to the sea bottom (e.g. Virnstein 1977). Such experiments, though they demonstrate that predation limits macrofaunal abundance, are subject to caging artifacts, especially in areas of high water flow.

A second method of determining the consequences of predation is to directly observe (or calculate from observations) the rate of prey consumption in the field. Pihl (1985), in a synthesis of studies performed on the Swedish west coast in 1977 and 1978, calculated the production and consumption of benthic invertebrates by five predators in two shallow (less than 1 m) bays. The predators were juvenile plaice (Pleuronectes platessa), two sand goby species (Pomatoschistus microps and P. minutus), brown shrimp (Crangon crangon) and crab (Carcinus maenas). These mobile epibenthic predators are opportunistic carnivores that feed mainly on infauna they select on the basis of relative availability. In one area, Gullmarsik, total food consumption in 1978 was calculated to be 26 g AFDW m^{-2} yr^{-1} (this corresponds to roughly 350 g wet weight). All epibenthic predators selected the amphipod, Corophium volutator, during most seasons. The predators consumed 98%,

62% and 92% of the annual production of C. volutator, M. arenaria and C. edule, respectively.

In a similar study on the Swedish west coast, Evans (1984) reported that Pleuronectes platessa, Pomatoschistus minutus and Crangon crangon consumed 24 to 34% of total infaunal production. These epifaunal predators consumed 67%, 60 to 80%, and 4% of the respective annual production of the important prey species, Corophium volutator, Crangon crangon and polychaete species, respectively. Phil's and Evans's studies indicate that, at least in shallow bays, epifaunal predators are major biotic regulators of the infaunal community.

A third method of inferring the consequences of predation is to correlate changes in the abundance of predator and prey populations over time. Persson (1981) established three lines of evidence suggesting that increased macrobenthic populations in the Baltic Sea resulted from thinning out of the flatfish stocks in the 1930s. Firstly, predator exclusion experiments in 1928 resulted in up to 60-fold increases in the density of preferred prey species. Secondly, surveys carried out following exploitation of the flatfish stocks indicated an increase in biomass of benthic macrofauna. Finally, the flatfish had increased growth rates, which Persson claimed to be a result of reduced competition for food.

Arntz (1980) analyzed eight years of data on the abundance of macrofauna and demersal fish in the Western Baltic Sea. Although fish preyed heavily on benthos, the abundance of one did not appear to depend on the abundance of the other. This does not necessarily mean that the abundances of fish and benthos are unrelated; it could be that they were not sampled closely enough in space and time, or that changes in population size were too small to show effects.

METHODS

This chapter is based, in part, on the yellowtail flounder stomach-content data presented in Chapter Two. Therein I described fish stomach collection and analysis; herein I add only those details pertaining to Chapter Three. In this chapter I use the data on stomach content weight (S) and percent composition of the diet by weight.

Fish stomach collection was standardized as much as possible given that the stomachs were collected by different people on a different ship each time. At each station, a No. 35 bottom trawl was towed every three hours, over a 24-hour period, in order to investigate diel feeding behavior. Tow duration (30 min) and speed (3.0 to 3.5 knots) were kept constant to enable comparison of the catch among stations and seasons. At each station and date, the temperature profile was measured by expendable bathythermograph and calibrated by a surface thermometer reading.

I estimated the consumption rate per fish by two methods: one based on bioenergetics, and the other on stomach contents. For the bioenergetic method, I used the consumption-to-biomass ratio (C/B) calculated for yellowtail flounder by Grosslein et al. (1980, Table 16). To get consumption per fish, I multiplied C/B by the mean weight of yellowtail flounder collected at Stations 5, 10 and 13 (Appendix B).

There are two alternate forms of the stomach-content method, which are based on the two alternate solutions of Eq. 3-2. The method I call change in stomach-content weight is based on Eq. 3-4. I calculated the mean stomach-content weight (S_t) for all stomachs, including empty ones, collected in each tow. Using Eq. 3-7 and the corresponding bottom temperature, I calculated the evacuation rate (r). I then applied Eq.

3-4 to each interval and summed over eight intervals to obtain the daily consumption rate.

In only two cases were enough fish stomachs collected to apply the change-in-stomach-content method; for the remaining stations and dates I relied on the mean-stomach-content method (Eq. 3-6). For each station and date, I calculated the mean stomach-content weight (S) from all stomachs, and the evacuation rate (r) by Eq. 3-7. The variance of consumption was calculated by propagating the variances of the mean stomach-content weights. I then interpolated the consumption rate between sampling dates and multiplied the mean consumption rate for each interval by the interval duration in days. Annual consumption is the sum of consumption during each quarterly sampling interval.

I estimated yellowtail flounder density by two different methods -- one direct and one indirect. In the first, I calculated density by dividing the area the otter trawl covered into the number of flounder caught. I estimated the area a standard tow covered by multiplying the ship speed times tow duration times the width of the net opening. Although this method gives a direct measure of abundance, it is an underestimate because the otter trawl does not catch every fish in its path.

Each year, since 1963, the Northeast Fisheries Center (NEFC) has conducted groundfish surveys along the northeast US coast from Cape Hatteras to the Gulf of Maine. These standardized, bottom-trawl surveys are done with NEFC research vessels in the fall -- and more recently, in the spring and sometimes summer -- of each year. Sampling is based on a stratified random design: the survey area has been stratified into zones based on depth and latitude (see Grosslein 1969, Fig. 2). Stations are allocated to each stratum in proportion to its area, and are located

within a stratum on a random basis. At each station, a standard, "36 Yankee" trawl is towed for 30 min at 6.5 km hr^{-1}.

I applied the Collie and Sissenwine (1983) method of estimating population size to yellowtail flounder groundfish-survey and commercial-catch data published in Clark et al. (1984, Tables 2, 4 and 5). This method estimates the number of fish in the area corresponding to the catch statistics. To get fish density per unit area, I divided population size by the area in which the population lives. I obtained the areas of the appropriate survey strata from Frank P. Almeida, NEFC (personal communication).

To calculate yellowtail flounder consumption per unit area, I multiplied the consumption rate per fish by yellowtail flounder density. The next step was to compare this food-consumption rate to the rates of prey production. In Chapter One, using the increment-summation method (Crisp 1984), I estimated the production of three dominant amphipod species. The species and the stations for which they were analyzed are: Ampelisca agassizi at Station 13 and Unciola inermis and Ericthonius fasciatus, both at Station 5-1 and at Station 5-28. M.C. Curran, also using the increment-summation method, estimated production of the sand dollar, Echinarachnius parma, at Stations 1, 4 and 10 (Collie and Curran 1985).

In this chapter I expand upon my previous production estimates by calculating the production of two polychaete species. As part of their life-history investigation, Blake and Baptiste (1985, Fig. 88) determined the size-frequency of Chone infundibuliformis in five quarterly samples taken at Staition 13 from July 1982 to July 1983. Because cohorts are not apparent in their size-frequency distributions, it was not possible to estimate production by cohort-based methods. Therefore, I used the

size-frequency (Hynes) method of estimating production, as modified by Krueger and Martin (1980).

In the size-frequency method the size distribution of an "average" cohort is obtained by averaging the frequencies in each size class over the year. Production (P) is then calculated as the sum of biomass removed between successive size classes, according to:

$$P = a[\quad (N_j - N_{j+1})(w_j w_{j+1})^{0.5}] \qquad (3.8)$$

where N_j is the mean number in size class j averaged over the sampling dates, w_j is the mean weight per individual of size class j, and a is the number of size classes.

Krueger and Martin (1980) recommended that the geometric mean weight, $(w_j w_{j+1})^{0.5}$, be used, because it is more accurate for logarithmic growth patterns. I used the length-weight regression for C. infundibuliformis (Table 2-2) to convert length to weight. The size-frequency method, though it does not rely on being able to identify cohorts in the size-frequency distributions, does assume that the average life-span is known. It also assumes that the growth rate is linear, that all individuals could grow to the maximum size and that the year-to-year population size is the same.

According to Wildish and Peer (1983), Chone infundibuliformis is an annual species; this is consistent with the length-frequency data in Blake and Baptiste (1985), which suggested that recruitment occurs in spring and early summer. Having estimated production of C. infundibuliformis at Station 13, I used the production-to-biomass ratio (P/B) to estimate production of this species at Station 5, from which samples of C. infundibuliformis were not measured.

I used the same approach to estimate production of Nephtys incisa at Station 13. This species was not measured in the GBMP, but N. incisa production at two other locations on the East Coast has been estimated. For Long Island Sound, Sanders (1956) calculated a production rate of 9.35 g wet weight m^{2} yr^{-1} and a P/B of 2.16. Off the Delaware coast, N. incisa production was 0.17 g ash-free dry weight m^{2} yr^{-1}, and P/B was found to be 2.23 (Howe and Leathem 1984). I applied these P/B values to the N. incisa mean biomass data from Station 13.

The final step is to calculate yellowtail flounder consumption as a function of prey production. The importance of the various prey species in the flounder diet on a weight basis was shown in Fig. 2-5. I calculated a weighted mean percent of each prey species in the diet by summing the weight of each prey species found in flounder stomachs over four seasons and dividing by the total weight of stomach contents (S). Next, I applied these percentages to the overall food consumption rate, to calculate the consumption rate of individual prey species. Finally I divided the consumption rate for each species by the corresponding prey production rate.

RESULTS

My first estimates of yellowtail flounder consumption rate were via the bioenergetic method. I used the C/B value of 4.6 yr^{-1} (Grosslein et al. 1980), which is a geometric mean for all ages during the years 1963 to 1972. The mean weights of yellowtail flounder, averaged over the year, caught at Stations 5, 10 and 13 were 348.1, 298.1 and 333.0 g, respectively (Appendix B). Multiplying by 4.6 yr^{-1}, I arrived at 1.60, 1.37 and 1.53 kg yr^{-1} $fish^{-1}$ for consumption at Stations 5, 10 and 13, respectively.

The second method of estimating consumption is based on the weights of the stomach bolus, which along with bottom temperatures are listed in Table 3-2. These total stomach-content weights differ from those listed in Appendix B (which do not include the weights of unidentifiable prey). Typically, the standard deviation of stomach-content weight is as large as the mean. The number of empty stomachs ranged from 8.3 to 65.4% of the total number examined; thus, some of the variation in stomach-content weight is due to the percentage of empty stomachs. In other words, there is less variability in mean stomach-content weight, among dates and stations, if only those fish with non-empty stomachs are considered.

In only two cases (August 1982 and May 1983 at Station 10) were enough stomachs collected to apply the change-in-stomach-content method. In Fig. 3-1 stomach-content weights (S_t) and 95% confidence intervals are plotted against the corresponding time of day. The large confidence intervals are due, in some cases (e.g. 8:40/August and 18:30/May) to small sample sizes (n = 8 and 7, respectively). In general, the variance of stomach-content weight is high because not all fish feed at the same time and there are many empty stomachs at any time of day.

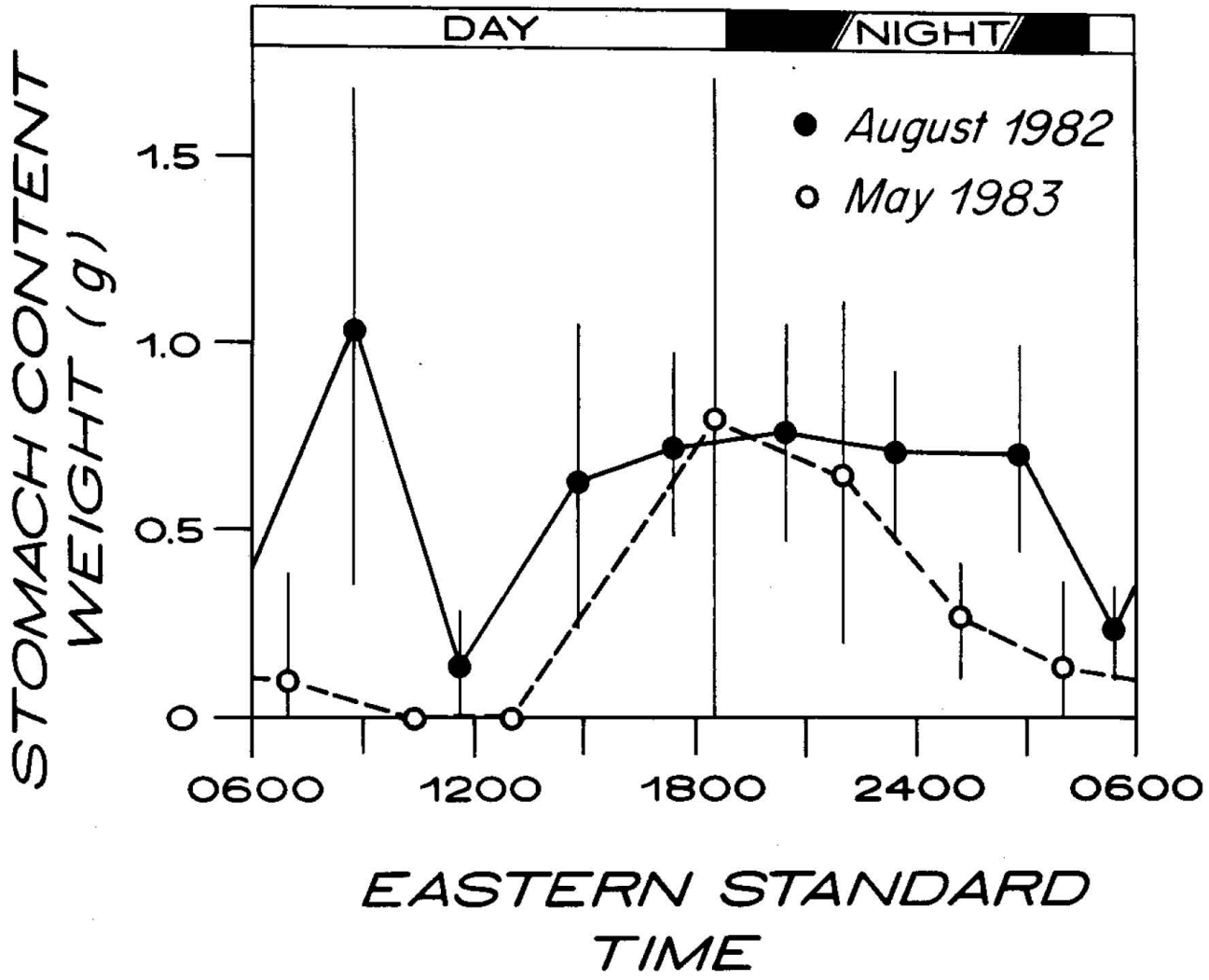


Figure 3-1. Change in yellowtail flounder stomach-content weight over 24 hours. The vertical lines are 95 percent confidence intervals.

Despite the high variance, there is a diel trend in stomach-content weight. If one ignores the anomalously high value for 8:40/August, stomach-content weight is lowest in the morning (6:00 to 12:00) and highest in the evening (18:00 to 24:00). This diel trend is apparent on both sampling dates. Because the confidence intervals for the two dates overlap at most times, there is no statistical difference between the August 1982 and May 1983 stomach-content weights.

I used Eq. 3-4 to estimate consumption during each time interval. The evacuation rates, as calculated from Eq. 3-7 and the temperatures given in Table 3-2, were 0.142 hr^{-1} and 0.097 hr^{-1} for August 1982 and May 1983, respectively. The ingestion rate was highest from 12:00 to 18:00, then continued at a low level until 24:00. The sum of consumption over 24 hours was 2.062 g day^{-1} and 0.760 g day^{-1} in Aug. 1982 and May 1983, respectively.

The mean-stomach-content method is applicable to the cases with smaller sample sizes. I estimated daily consumption using Eq. 3-4 and the mean stomach-content weights (S) given in Table 3-2. Evacuation rates (r) were calculated using Eq. 3.7 and the bottom temperatues from Table 3-2. Daily consumption is plotted, in Fig. 3-2, against time of year. I calculated 95% confidence intervals by propagating the variance of mean stomach-content weight. The large confidence intervals are due, in some cases, to small sample sizes, the diel feeding cycle (as illustrated in Fig. 3-1), and, more generally, to the variation in feeding behavior among fish. As expected, for August 1982 and May 1983 at Station 10, the consumption rates calculated by the change-in-stomach-content method are identical to those calculated by the mean-stomach-content method.

Annual consumption, obtained by interpolating between sampling dates,

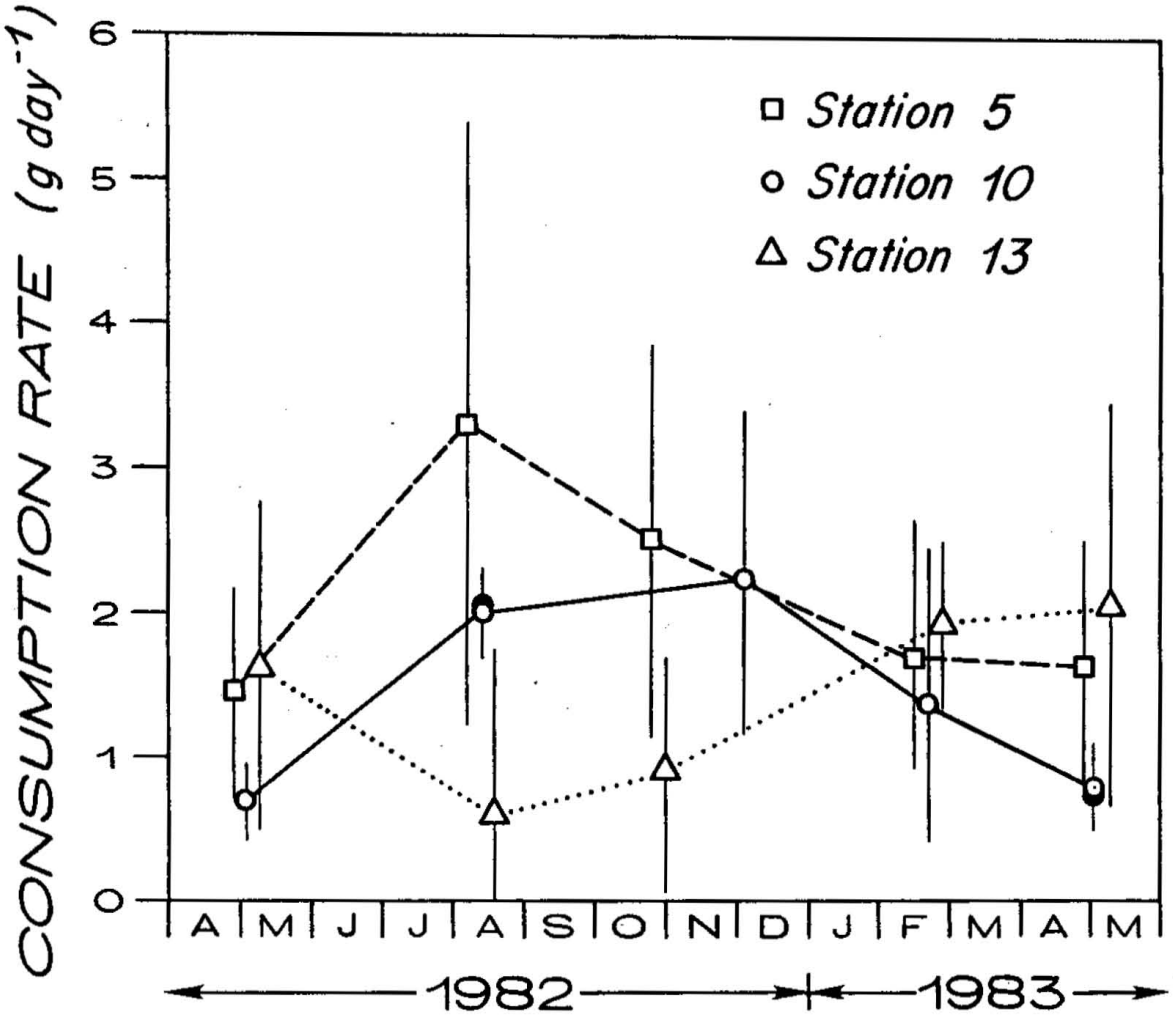


Figure 3-2. Rate of food consumption by yellowtail flounder estimated by the mean-stomach-content method. Units are grams wet weight per day. The vertical lines are 95 percent confidence intervals. The partially eclipsed solid dots represent consumption estimated by the change-in-stomach-content method. (See text for explanation of methods.)

corresponds to the area under each line in Fig. 3-2. Annual consumption was 0.824, 0.605 and 0.477 kg fish^{-1} yr^{-1} at Stations 5, 10 and 13 respectively. Because of the large variance in daily consumption, these values are probably not statistically different from one another. They are, however, about half or less than half the consumption rates estimated by the bioenergetic method (Table 3-4).

I estimated yellowtail flounder density based on the area trawled and from catch statistics. The standard tow of 30 min. at 3.0 knots covered a distance of 2.78 km. The opening of the otter trawl, when fishing, is about 9.5 m (Frank P. Almeida, pers. comm.). Therefore, the area covered by a standard tow was 2.64×10^4 m^2. To calculate flounder density I first divided the catch by the area of one standard tow and then by the number of standard tows made at that station and date. The density estimates (Table 3-3) are all quite low; there are no consistent trends among stations or dates. It should be remembered that these are minimum estimates because the trawl does not catch every fish in its path.

I also estimated flounder density based on the area trawled by the NEFC groundfish survey. Benthic Monitoring Stations 5 and 10 are in Survey Stratum 13; Monitoring Station 13 is in Stratum 10. I divided the minimum population estimates for these two strata (Margaret McBride, unpublished data) by the appropriate area, to obain the densities listed in Table 3-3. These values are still low but are higher than the densities obtained on the stomach-sampling cruises. In other words, the mean catch-per-tow from the survey strata was generally higher than the catch-per-tow from specific monitoring stations.

As an indirect method of estimating yellowtail flounder density, I applied the Collie and Sissenwine (1983) method to a 21-yr time series (1963-1983) of commercial-catch and research-survey data (Clark et al.

Table 3-2. Yellowtail flounder stomach-content weights.

Date	Station	Content weight (g) Mean	S.D.	No. of stomachs Total	Non-empty	Bottom Temp. (°C)
August 1982	5	1.179	1.188	12	11	9.5
	10	0.592	0.711	244	176	11.3
	13	0.165	0.422	10	4	12.1
October 1982	5	0.893	1.355	33	21	9.5
December 1982	10	0.702	1.126	42	29	10.8
October 1982	13	0.186	0.432	26	9	14.3
February 1983	5	0.852	0.876	17	11	6.6
	10	0.730	0.690	9	6	6.3
	13	0.993	0.945	42	37	6.2
May 1983	5	0.816	1.101	30	24	6.5
	10	0.340	0.561	102	51	7.9
	13	0.912	1.576	27	21	7.5

Table 3-3. Yellowtail flounder density (fish hectare^{-1})*.

Method	Date	Station 5	10	13
Area trawled (stomach-collection cruises)	August 1982	0.42	11.74	0.27
	Oct., Dec. 1982	0.97	1.99	0.75
	February 1983	1.20	0.43	2.48
	May 1983	0.87	2.66	2.05
Area trawled (research survey)	Fall 1982	5.30	5.30	1.90
Catch data	Fall 1982	20.07	20.01	41.34

* 1 hectare = 10^4 m^2)

1984). The research-survey data come from the fall groundfish survey and are expressed as mean number per standardized tow; the commercial-catch data are simply numbers landed. There are five major yellowtail flounder fishing grounds: Gulf of Maine, Cape Cod, Georges Bank, Southern New England and Mid Atlantic. These populations are more or less discrete and their catch statistics are compiled separately. Stations 5 and 10 are on Georges Bank and Station 13 is in the area inhabited by the Southern New England population. Therefore, I estimated the size of both these populations.

This method smooths the relative abundance index and estimates a catchability coefficient relating the mean catch-per-tow to total population size. Observed and estimated catches per-tow-are plotted, for the Georges Bank and Southern New England populations, in Figs. 3-3 and 3-4, respectively. Population size is obtained by dividing the estimated relative-abundance index by the catchability coefficient. The population estimates, for fall 1982, are: 64.9 million fish for Georges Bank and 117.0 million fish for Southern New England.

These population estimates apply to the area from which the commercial catch was taken. This area is bounded by the 100-m isobath because yellowtail flounder are rarely caught below this depth (Lux and Livingston 1982). I summed the areas of the appropriate survey strata for each of the two flounder populations. The survey strata corresponding to the Georges Bank population are numbers 13, 16, and 19 to 21, with a total area of 32,329 km^2. Yellowtail flounder density on Georges Bank in fall 1982 was thus 20.07 fish $hectare^{-1}$. For the Southern New England population, the corresponding survey strata are numbers 5, 6, 9 and 10 with a total area of 28,294 m^2. This gives a 1982 yellowtail flounder density of 41.34 fish $hectare^{-1}$.

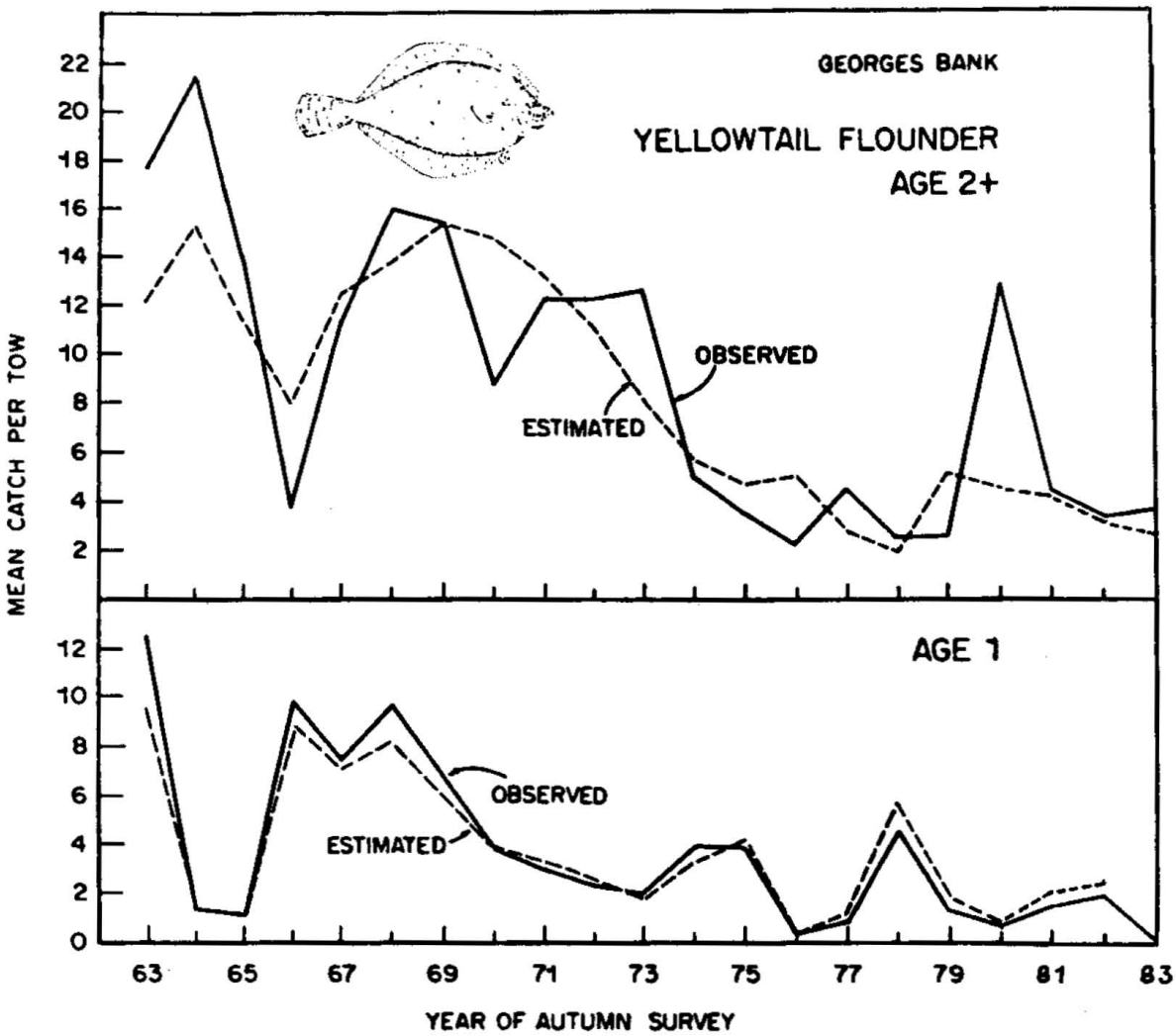


Figure 3-3. Relative abundance of Georges Bank yellowtail flounder in the NEFC groundfish survey. Redrawn from Collie and Sissenwine (1983).

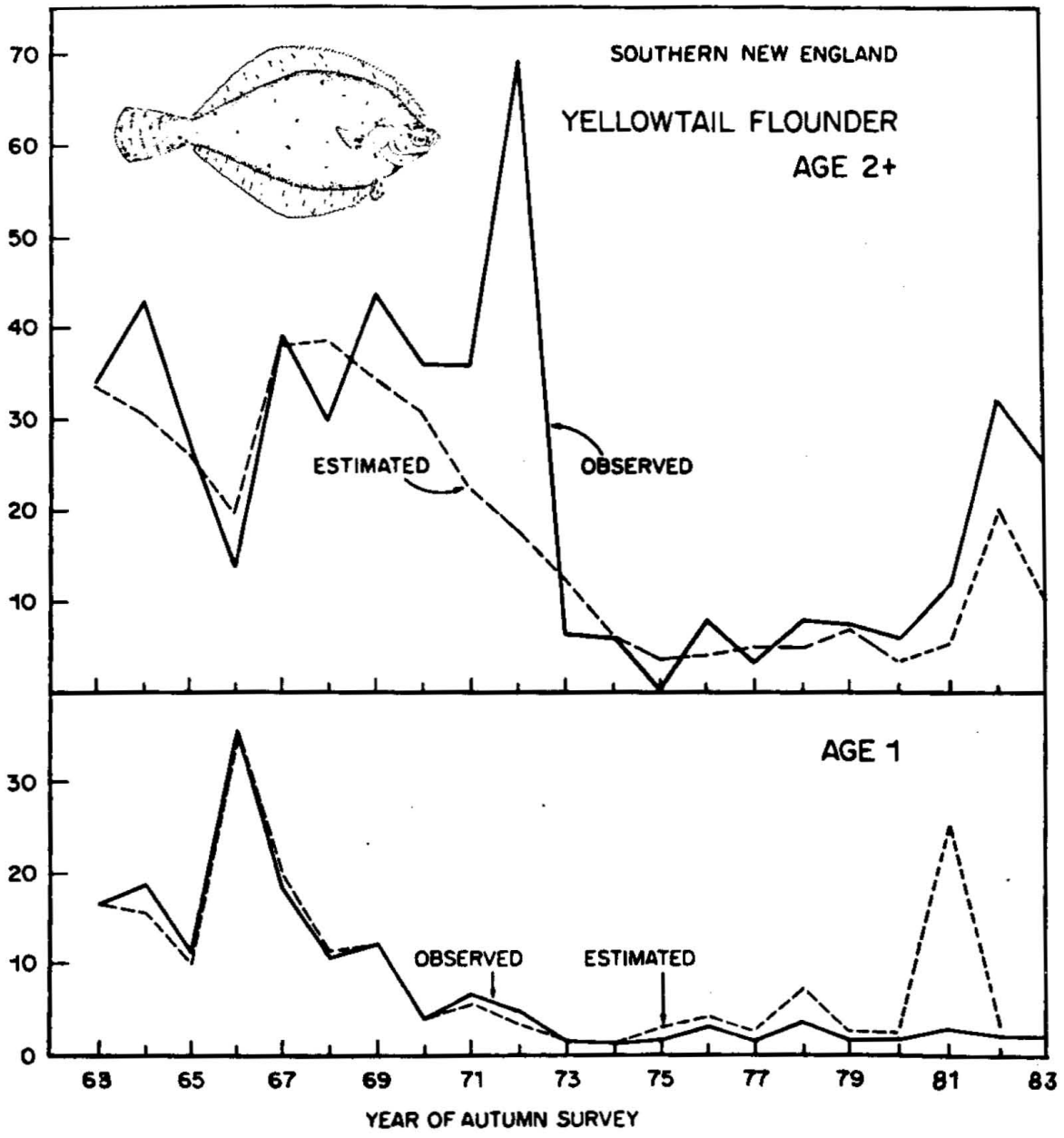


Figure 3-4. Relative abundance of Southern New England yellowtail flounder in the NEFC groundfish survey. Redrawn from Collie and Sissinwine (1983).

Yellowtail flounder density as estimated by the Collie and Sissenwine method is substantially higher than those estimates based on area trawled (Table 3-3). This is not surprising because the latter method is known to underestimate true density. I have used the catch-data estimates in subsequent calculations. To calculate consumption rate per unit area, I multiplied these density estimates by the consumption rate per fish. I used the estimates based on stomach contents as lower ranges of consumption and the estimates based on bioenergetics as upper ranges. This, in turn, gives a range for consumption per unit area (Table 3-4).

Annual production rates of six important prey species are listed in Table 3-5. The amphipod production rates, in wet-weight units, are from Appendix A. I used the mean of production at Stations 5-1 and 5-28 for Unciola inermis and Ericthonius fasciatus. Data for the sand dollar, Echinarachnius parma, are listed in Collie and Curran (1985). I took the E. parma annual production rate from Table 20 and converted it to grams wet weight using the composition data in Table 19.

Pooled size-frequency data for Chone infundibuliformis at Station 13 are plotted in Fig. 2-10. I standardized the frequencies from the benthic grab samples to number per m^2 before applying the size-frequency method (Eq. 3-8) to estimate production. The production and biomass calculations are given in full in Appendix C; production was 6.60 g wet weight (ww) m^{-2} yr^{-1} and P/B was 2.83 yr^{-1}.

I used this P/B value to estimate C. infundibuliformis production at Station 5 (from where size measurements were not made). Mean C. infundibuliformis biomass at Stations 5-1 and 5-28 was 0.468 gww m^{-2}. I multiplied this figure by 1.15 to account for weight loss due to preservation of the worms in alcohol, and multiplied the corrected biomass by P/B to get the production estimate of 1.52 gww m^{-2} yr^{-1}.

Table 3-4. Yellowtail flounder consumption rates (wet weight).

	Station 5	Station 10	Station 13
Consumption per fish (kg yr^{-1})			
Bioenergetic method	1.60	1.37	1.53
Stomach-content method	0.82	0.60	0.48
Yellowtail flounder density (fish m^{-2})	2.01×10^{-3}	2.01×10^{-3}	4.13×10^{-3}
Consumption per unit area (g m^{-2} yr^{-1})	1.65-3.23	1.22-2.75	1.98-6.32

Table 3-5. Yellowtail flounder consumption as a percentage of prey production. (gww = grams wet weight)

Prey species	Station	Production (gww m^{-2} yr^{-1}) Jul 82-Jul 83	Percent of flounder diet (by weight)	Consumption / Production (%)
Unciola inermis	5	8.93	31.8	5.88-11.50
Ericthonius fasciatus	5	13.08	18.8	2.37- 4.64
Chone infundibuliformis	5	1.52	9.8	10.64-20.83
C. infundibuliformis	13	6.60	35.4	10.62-33.90
Nephtys incisa	13	6.02	20.1	6.61-21.10
Ampelisca agassizi	13	11.58	5.2	0.89- 2.84
Echinarachnius parma	10	97.14	2.6	0.03- 0.07

I used the same approach to estimate production of Nephtys incisa at Station 13. Again, I multiplied the mean biomass of 2.285 gww m^{-2} yr^{-1} by 1.15 before applying the P/B values of 2.16 (Sanders 1956) and 2.23 (Howe and Leathem 1984). The resulting production estimate ranges from 5.92 to 6.12 gww m^{-2} yr^{-1}; I used the mean value (Table 3-5) in subsequent calculations.

Fig. 2-5 shows the mean biomass per flounder stomach of the five most important prey species at each station. These data, converted to percent of total stomach-content weight, are listed in Table 3-5. I applied these percentages to consumption per unit area as listed for each station in Table 3-4. Finally, I divided the consumption rates for each species by the corresponding prey production rates to obtain the final column of Table 3-5. Consumption as a percent of prey poduction was highest for the two polychaete species, intermediate for the three amphipod species, and insignificantly low for the sand dollar.

DISCUSSION

The diel pattern in stomach-content weight (Fig. 3-1) is consistent with that reported in two previous studies of yellowtail flounder food habits. Bowman (1980) studied the feeding chronology of demersal fish at a site on southern Georges Bank situated about midway between Stations 5 and 10. Yellowtail flounder stomachs were fullest between 18:00 and 21:00 hours; stomach-content weight decreased from 21:00 to 3:00 hours (Bowman 1980, Fig. 5). Surprisingly, smaller flounder (mean 23 cm) had more food in their stomachs than larger (mean 36 cm) flounder. Langton (1983) studied the food habits of yellowtail flounder collected during NEFC groundfish surveys from 1973 to 1976. Stomach-content weight was highest from 15:00 to 21:00 hours and lowest from 3:00 to 12:00 hours (Langton 1983, Fig. 1).

These two studies and my results indicate that yellowtail flounder are daytime feeders with peak food consumption in the afternoon to early evening hours. Some flounder probably feed at a slower rate throughout the day and night. In the evening, stomach contents accumulate faster than they are digested, resulting in the stomach-content weight maximum. Bowman (1980) suggested that yellowtail flounder are visual feeders that also use olfaction to locate their prey.

Catchability of yellowtail flounder is higher at night than during the day (Bowman 1980). My results confirm this pattern in that catches were higher at night than day. It is unclear whether increased catchability at night is due to increased activity or to decreased avoidance.

The change-in-stomach-content method of estimating consumption is equivalent to the mean-stomach-content method provided that stomach-

content weight is roughly the same at the beginning and end of the feeding cycle. In my study, the assumption of a diel feeding pattern was fulfilled and the two methods produced similar results in the two cases to which they both were applied. This justified the use of the mean-stomach-content method in cases with small sample sizes.

Langton (1983) found that yellowtail flounder, mean stomach-content weight was higher in the spring, prior to spawning, than in the fall and that mean weight per stomach was higher on Georges Bank than in the Southern New England area. Efanov and Vinogradov (1973) also noted that yellowtail flounder feed more intensively on Georges Bank than they do in Southern New England. My consumption-rate estimates, based on stomach contents (Table 3-4), are consistent with the two previous studies. Consumption at Station 13 (Southern New England) was lower than consumption at Stations 5 and 10 (Georges Bank).

Consumption, as estimated by Eq. 3-6, is the product of mean stomach-content weight and evacuation rate. At Station 13, mean stomach-content weight was higher in the spring, prior to spawning, but this trend was not apparent at the other two stations. Because the evacuation rate is a function of temperature, it is higher in summer and fall than in winter and spring. No clear seasonal trend in consumption rate is apparent in Fig. 3-2. Consumption at Stations 5 and 10 was highest in summer and fall owing to the warm temperatures, while consumption at Station 13 was lowest in summer and fall because of low stomach-content weights.

Jones (1978) calculated annual consumption of cod and haddock based on energy requirements and on stomach-content weights. Both methods gave results of the same order of magnitude, and there was no systematic difference between the two. For haddock, the bioenergetic method gave a higher consumption estimate than the stomach-content method; for cod, the

reverse was true. In my study consumption estimates based on bioenergetics were at least twice as high as estimates based on stomach contents. The main uncertainty in the bioenergetic method is in estimating the amount of respiration due to activity. Grosslein et al. (1980) assumed that active metabolism requires twice the energy of resting metabolism.

Compared to the other consumption rates in Table 3-1, especially those for winter flounder, the bioenergetic estimate for yellowtail flounder does not seem too high. It is more likely that the stomach-content estimates are too low. The fish stomachs were fixed in formalin and transferred to alcohol before the contents were weighed; one explanation for the low estimates is that the preservatives could result in a weight loss of 15% or more (Mills et al. 1982).

The population-density estimates based on area trawled, though not useful in calculating consumption per unit area, indicate the efficiency of the otter trawl and the relative catchability of flounder at different seasons and sites. Comparing the minimum population estimates from the fall 1982 survey to those based on catch data, I calculated that the otter trawl was 10 to 25% efficient in catching yellowtail flounder. Flounder catch-per-tow on the stomach-collection cruises was usually lower than catch-per-tow in the same stratum on the groundfish survey. This observation highlights out the difficulty in obtaining repeated catches of a mobile, migratory predator from fixed locations.

The population abundances based on catch statistics cannot be gross overestimates because there must have been at least as many yellowtail flounder as the number caught commercially. The main weakness in this approach is that the estimates of flounder density apply to several survey strata that may not equally represent the benthic monitoring

stations. Although catch per tow is tabulated stratum by stratum, there is no obvious way of weighting the Collie and Sissenwine (1983) method in order to estimate fish abundance in one particular stratum.

A potential source of error in the Chone infundibuliformis data is that C. infundibuliformis is difficult to distinguish from the similar, but smaller, congeneric species, C. duneri. Juvenile C. infundibuliformis may have been misidentified or not identified to species (Blake and Baptiste 1985). This identification problem does not invalidate the C. infundibuliformis results in this thesis, provided that Chone in the fish stomachs were identified by the same criteria as those in the grab samples. If I assume, for sake of arguement, that all large Chone were called C. infundibuliformis and all small ones were called C. duneri, it would be the same as having two size groups of one species. If juveniles were misidentified, the estimate of C. infundibuliformis production may be two low, but it still applies to the size range eaten by flounder. The P/B value of 2.83 yr^{-1} is as high as the P/B values of other annual species, so this potential underestimate may not be important.

The results in Table 3-5 imply that food consumption by yellowtail flounder is not limited by prey production because there is excess prey production not utilized by flounder. Figs. 3-3 and 3-4 show that yellowtail flounder population size was much lower from 1981 to 1983 compared to the earlier period, 1963 to 1965. The flounder population is especially reduced on Georges Bank; in the Southern New England area, flounder abundance has increased thanks to the strong 1980 year class. According to Grosslein et al. (1980), yellowtail flounder consumption per unit area on Georges Bank was 5.8 g m^{-2} yr^{-1} from 1964 to 1966 and 4.4 g m^{-2} yr^{-1} from 1973 to 1975.

Using my population estimates I calculated consumption by flounder as 6.0 to 11.7 g m^{-2} yr^{-1} in 1963. My estimates are higher than those of Grosslein et al. (1980) because, in calculating flounder density, I used the area of strata where yellowtail flounder are caught instead of the entire area of Georges Bank. At the 1963 population level, if consumption rate per fish and prey-production rates equalled 1982 levels, the consumption rates in Table 3-5 would be increased by a factor of 3.6. Given these assumptions, yellowtail flounder would consume 21.2 to 41.4%, 8.5 to 16.7% and 38.3 to 75.0% of the annual production of Unciola inermis, Ericthonius fasciatus and Chone infundibuliformis, respectively. At these consumption levels, prey production could limit feeding.

If yellowtail flounder feeding were limited by prey production, one would expect that the hypotheses Persson (1981) proposed for the Baltic Sea would apply to Georges Bank. These hypotheses state that as flounder abundance decreases, individual growth rates should increase because of decreased competition for food, and the biomass of benthic macrofauna should increase. To test the growth-rate hypothesis, I plotted mean length at age of yellowtail flounder caught during the fall groundfish survey from 1963 to 1983 (Fig. 3-5). I plotted mean lengths for ages 1, 2 and 3 only, because the sample sizes of older ages are too small. On the average, mean lengths-at-age were higher from 1974 to 1983 when flounder were less abundant, and lower from 1963 to 1973 when flounder were more abundant. However, there is a good deal of year-to-year variability not explained by the density-dependent growth rate hypothesis.

Although several Georges Bank surveys have measured benthic biomass (e.g. Wigley 1968, Michael et al. 1983, Battelle and WHOI 1984), a direct comparison of the results is hampered by the fact that different stations were sampled and different methods were used on each survey. One problem

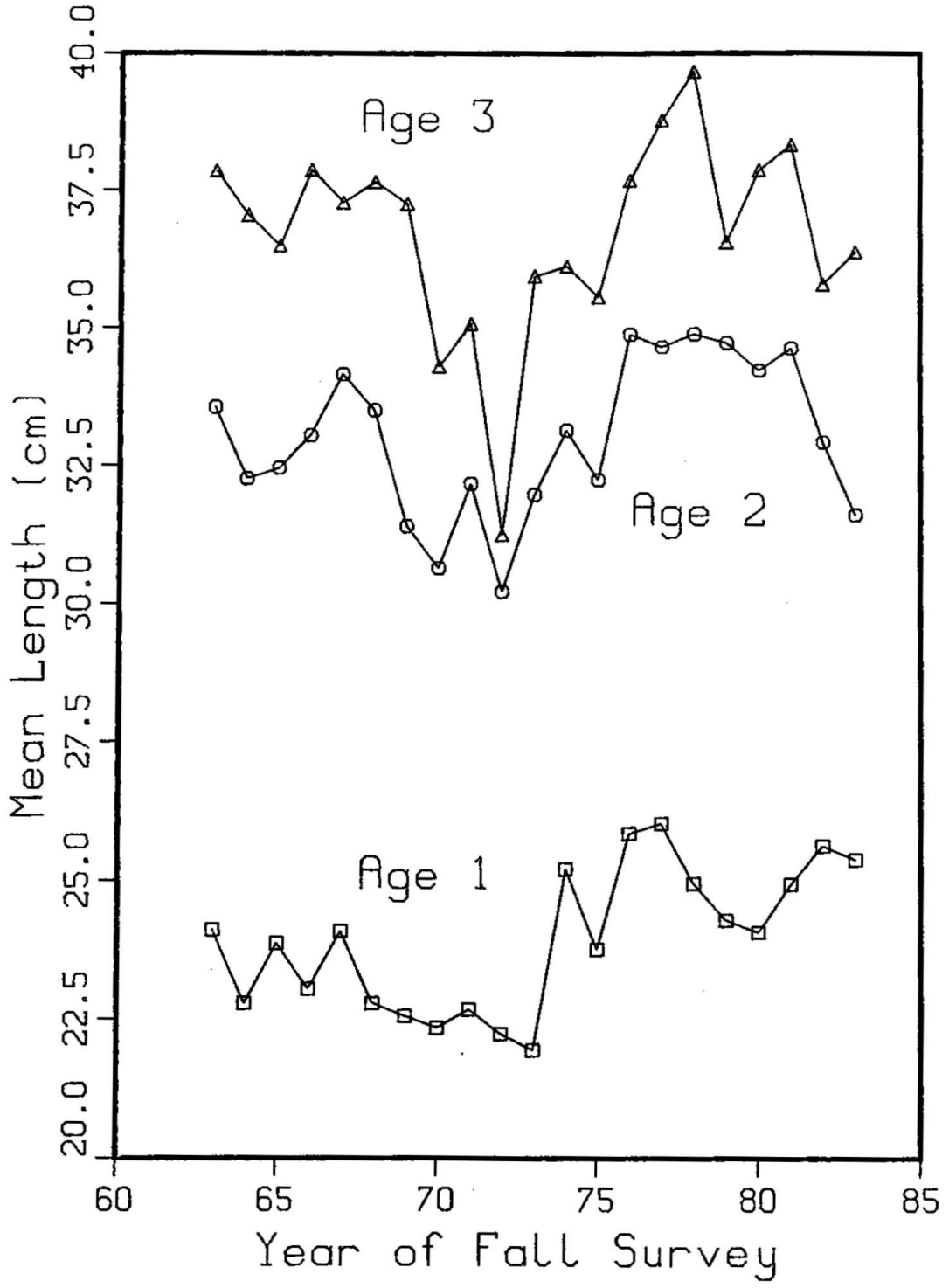


Figure 3-5. Mean length-at-age of Georges Bank yellowtail flounder in the NEFC groundfish survey. These data were provided courtesy of Margaret McBride, NEFC.

with wet-weight biomass data is that a few large species with hard parts, such as Arctica islandica and Echinarachnius parma, completely dominate the biomass. Only juveniles of these species are small enough for flounder to eat. Even if the weights of these large species are excluded, methodological differences preclude a valid comparison among benthic surveys. On more recent surveys, increasingly finer sieves, which retain more animals, have been used. Thus, biomass may appear to increase regardless of real changes in the benthos.

The results in Table 3-5 show that yellowtail flounder consume a significant proportion (up to 33%) of the production of important prey species. To some extent, flounder may thus regulate the abundance of benthic macrofauna. What is the fate of the remaining portion of prey production, not consumed by flounder? Much of the production is probably consumed by other fish and by invertebrate species.

Following is a list of some benthivorous fish species and their diet compositions as analyzed by Bowman and Michaels (1984). The numbers in parentheses are percentages by weight of different food types in the predator's diet. Amphipod feeders include little skate (14.0%), haddock (7.5%), red hake (5.0%) and scup (7.2%). Ampelisca spp., Unciola spp. and Ericthonius spp. were among the most numerous prey of these fish. Additionally, the juveniles of some fish, such as cod and silver hake, feed on amphipods, switching to larger prey as adults.

Polychaete feeders include little skate (10.7%), haddock (18.1%), scup (39.1%), butterfish (12.8%) and witch flounder (62.1%). Worms of the families Sabellidae, Nephtyidae and Lumbrineridae were important prey for these fish. Two fish species that specialize in eating the sand dollar, Echinarachnius parma, are ocean pout (82.5%) and American plaice (66.2%).

Although the diets of these fish species are well documented, consumption rates and abundances can be calculated only for a few of them. The combined predation by this guild of benthic-feeding fish may be substantially more than that of yellowtail flounder alone. Together, these predators could regulate the abundance of their benthic prey.

CONCLUSIONS

Results of the life-history analysis aided in interpreting changes in species abundance observed during the Georges Bank Benthic Infauna Monitoring Program. Much of the variation in amphipod abundance was explained on the basis of recruitment and subsequent mortality, although adult migration may be important in explaining population changes in Ericthonius fasciatus. Production of benthic amphipods at the stations investigated was as high (1.3 to 3.2 gdw m^{-2} yr^{-1}) as production by related near-shore species with similar life-spans. The seasonal variation in amphipod growth rates (Fig. 1-8) can be fit remarkably well by a sine curve (not shown) that is in phase with the annual primary production cycle on Georges Bank (O'Reilly et al., in press). The high production rates and coupling of amphipod growth to primary production indicate that phytodetritus reaches the bottom and is utilized by amphipods.

Stomach-content analysis confirmed the importance of benthic macrofauna in the diet of yellowtail flounder on Georges Bank. Although the flounder diet is broad, feeding is by no means random. Yellowtail flounder select suitably sized prey that live on or near the sediment surface. The composite size-selection curve (Fig. 2-15) is consistent with Andersen's (1982) hypothesis of a log-normal selection function.

Different prey species dominated the yellowtail founder diet at different dates and stations. The selectivity indices showed that, in general, diet composition changed seasonally in relation to variations in benthic species abundance. This means that predation patterns are predictable on the basis of prey species and prey size. There was, however, residual variation in diet composition not explained by

selection indices. Pelagic prey were eaten in the absence of suitable benthic prey.

I estimated yellowtail flounder consumption rates with two different methods. The method based on bioenergetics gave consistently higher results (1.4 to 1.6 kg fish^{-1} yr^{-1}) than the method based on stomach-content weight (0.5 to 0.8 kg fish^{-1} yr^{-1}). Using estimates of yellowtail flounder density (Table 3-4), I converted these consumption rates to consumption per unit area. At 1982 population densities, prey production did not appear to limit flounder feeding (Table 3-5) although yellowtail flounder may compete for prey with other benthic feeders. Prey production may have limited feeding in the 1960s when yellowtail flounder were more abundant than at present (Figs. 3-3 and 3-4). There is slight evidence that flounder growth rates have increased in response to lower population densities (Fig. 3-5). Predation by yellowtail flounder is a small but significant source of mortality on the prey populations (Table 3-5). Consumption by all benthic-feeding fish species could account for most of the prey production.

Together, the three chapters present a consistent picture of the prey species' life-history strategies. Chapter Two showed that predation on amphipods was highly size selective. Yellowtail flounder selected adult aphipods and neglected the juveniles. The mortality rates of adult amphipods (Figs. 1-3 to 1-5) appear to be higher than the mortality rates of juveniles. This observation is consistent with the size-selective pattern of flounder predation.

Of the three amphipod species, Ampelisca agassizi lives longest, grows slowest, and has the lowest P/B (Table 1-7). The tubes of A. agassizi extend vertically into the substratum, providing a refuge from predation. Compared to the other amphipod species, A. agassizi is

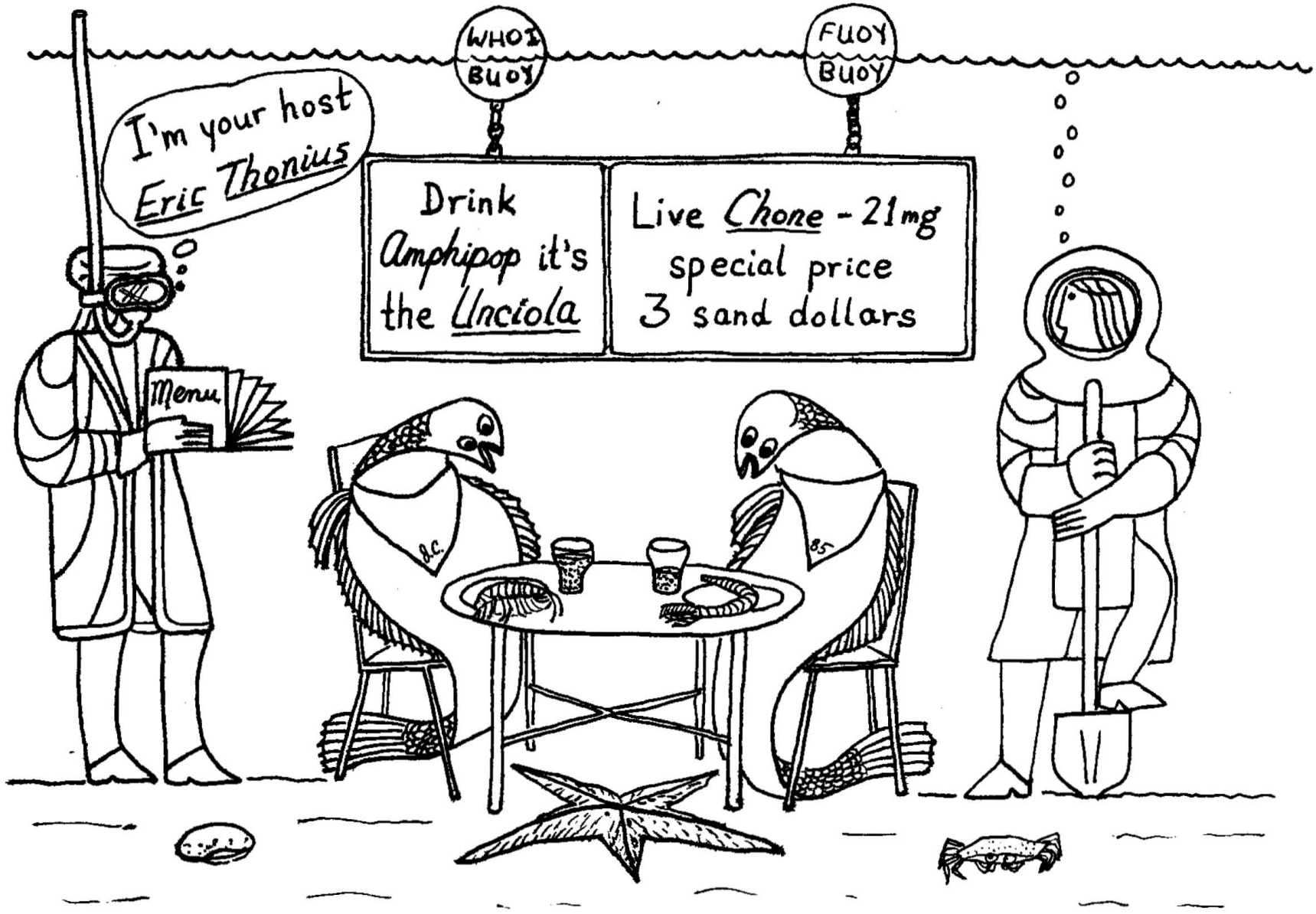
selected against at all sizes (Fig. 2-15) and only a small proportion of its annual production is consumed by yellowtail flounder (Table 3-5).

In contrast, Ericthonius fasciatus has the shortest life-span, fastest growth rate and highest P/B. E. fasciatus is an epifaunal tube builder and is thus more vulnerable to predation. Compared to the other two amphipod species, E. fasciatus is selected for at all lengths. However, E. fasciatus does not grow as big as the other species and much of its production occurs in the small size classes not preferred by flounder.

Unciola inermis is intermediate in these life-history traits. Its tubes are usually built into the substratum and are thus less exposed to predation. U. inermis grows to a larger maximum weight than the other amphipods and therefore, more of its production is in the size classes preferred by flounder. In summary, the trade-off between growth rate and life-span seems to be mediated by predation.

Yellowtail flounder, eating intermediate sizes of Echinarachnius parma (Fig. 2-9), accounted for an insignificant proportion of annual sand dollar production (Table 3-5). Most E. parma are too large for flounder to eat. Fish predation on intermediate-sized sand dollars could account for the absence of those sizes in the benthos and thus for the periodic recruitment pattern exhibited by E. parma.

The polychaete, Chone infundibuliformis, appears to be the optimal prey size -- all its size classes were positively selected by yellowtail flounder (Fig. 2-15). Of the six prey species in listed Table 3-5, C. infundibuliformis had the highest proportion of its production consumed by flounder. Thus, the selection index, as calculated in Chapter Two, is consistent with the impact of predation, as calculated in Chapter Three.


WHOI BUOY
FUOY BUOY
I'm your host Eric Thonius
Drink Amphipop it's the Unciola
Live Chone - 21mg special price 3 sand dollars
Menu

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Appendix A. *Ampelisca agassizi* production (wet weight) at Station 13 from July 1981 to July 1982.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $N\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
80A	Jul	154.2	6.95	0.70	3.76	579.8	-	-	-
	Nov	114.4	7.19	0.68	4.11	470.2	0.35	134.3	47.0
	Feb	164.6	7.64	0.34	4.77	785.1	0.66	139.5	92.1
	May	12.1	9.28	0.20	5.91	71.5	1.14	88.4	100.7
	Jul	31.1	9.43	0.49	8.44	262.5	2.53	21.6	54.6
80B	Jul	44.8	4.34	0.60	1.08	48.4	-	-	-
	Nov	77.5	6.21	0.48	2.83	219.3	1.75	61.2	107.0
	Feb	176 0	6.26	1.10	2.97	522.7	0.14	126.8	17.7
	May	7.8	7.49	0.25	4.51	35.2	1.54	91.9	141.5
	Jul	27.8	8.60	0.18	6.54	181.8	2.03	17.8	36.1
81A	Nov	181.3	2.42	0.56	0.24	43.5	-	-	-
	Feb	298.6	3.52	0.80	0.66	197.1	0.42	240.0	100.8
	May	46.9	4.99	1.14	1.68	78.8	1.02	172.8	176.2
	Jul	278.4	6.35	0.81	2.99	832.4	1.31	162.7	231.1
81B	Feb	215.9	2.40	0.32	0.22	47.5	-	-	-
	May	84.3	2.91	0.58	0.38	32.0	0.16	150.1	24.0
	Jul	238.8	4.68	0.67	1.32	315.2	0.94	161.6	151.9

Total production:	1.26 g 0.24 m^{-2} yr^{-1}	5.26 g m^{-2} yr^{-1}
Total biomass:	4.72 g 0.24 m^{-2}	19.68 g m^{-2}
Mean biomass:	0.95 g 0.24 m^{-2}	3.93 g m^{-2}
Production/mean biomass:		1.34 g yr^{-1}

Appendix A. *Ampelisca agassizi* production (wet weight) at Station 13 from July 1982 to July 1983.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $N\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
80A	Jul	31.1	9.43	0.49	8.44	26.2	-	-	-
80B	Jul	27.8	8.61	0.18	6.56	182.4	-	-	-
81A	Jul	278.4	6.35	0.81	2.99	832.4	-		
	Nov	190.0	7.46	0.43	4.49	404.1	1.50	184.2	276.3
	Feb	122.7	7.94	0.74	5.37	658.9	0.88	106.4	93.6
81B	Jul	238.8	4.68	0.67	1.32	315.2	-	-	-
	Nov	199.9	6.47	0.47	3.07	613.7	1.75	219.4	383.9
	Feb	239.3	6.94	0.55	3.72	890.2	0.65	219.6	142.7
	May	148.1	8.00	0.78	5.49	813.1	1.77	193.7	342.8
	Jul	148.8	8.12	0.57	5.66	842.2	0.17	148.5	25.2
82A	Nov	356.9	4.09	0.50	0.91	324.8	-	-	-
	Feb	574.1	5.11	0.63	1.66	953.0	0.75	465.5	349.1
	May	403.1	6.92	1.00	3.81	1535.8	1.15	488.6	561.9
	Jul	115.0	6.95	0.32	3.70	424.5	0.11	259.1	-28.5
82B	Nov	295.7	2.34	0.34	0.20	59.1	-	-	-
	Feb	544.2	2.55	0.44	0.26	141.5	0.06	420.0	25.2
	May	458.0	3.97	0.67	0.86	393.9	0.60	501.1	300.7
	Jul	298.5	5.11	0.68	1.67	498.5	0.81	378.3	306.4

Total production:	2.78 g 0.24 m^{-2} yr^{-1}	11.58 g m^{-2} yr^{-1}
Total biomass:	9.91 g 0.24 m^{-2}	41.29 g m^{-2}
Mean biomass:	1.98 g 0.24 m^{-2}	8.26 g m^{-2}
Production/mean biomass:		1.40 g yr^{-1}

Appendix A. *Unciola inermis* production (wet weight) at Station 5-1 from July 1981 to July 1982.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
80A	Jul	9.8	8.80	0.21	10.92	107.0	-	-	-
80B	Jul	122.3	7.23	0.43	6.75	325.5	-	-	-
	Nov	13.8	9.59	0.31	13.53	186.7	6.78	68.1	461.7
81A	Jul	230.6	4.03	0.78	1.68	387.4	-	-	-
	Nov	55.0	7.07	1.17	6.66	366.3	4.98	142.8	711.1
	Feb	8.4	7.57	0.37	7.54	63.3	0.88	63.4	55.8
	May	29.2	9.29	0.77	12.64	369.1	5.10	18.8	95.9
	Jul	51.6	3.92	0.75	11.43	589.8	-1.21	40.4	-48.9
81B	Jul	265.2	2.32	0.53	0.44	116.7	-	-	-
	Nov	227.1	4.48	0.92	2.21	501.9	1.77	246.2	435.8
	Feb	226.9	3.94	0.66	1.56	354.0	-0.65	227.0	-147.6
	May	117.9	7.19	0.73	6.74	794.6	5.18	172.4	893.0
	Jul	59.8	7.45	0.42	7.26	434.1	0.52	88.9	46.2
82A	May	49.7	2.88	0.59	0.74	36.8	-	-	-
	Jul	11.1	5.91	0.19	4.07	45.2	3.33	30.4	101.2
82B	May	335.3	1.49	0.18	0.14	46.9	-	-	-
	Jul	297.2	3.73	0.82	1.41	419.1	1.27	316.3	401.7

Total production:	3.01 g 0.24 m^{-2} yr^{-1}	12.52 g m^{-2} yr^{-1}
Total biomass:	5.64 g 0.24 m^{-2} yr^{-1}	23.52 g m^{-2}
Mean biomass:	1.13 g 0.24 m^{-2} yr^{-1}	4.70 g m^{-2}
Production/mean biomass:		2.66 g yr^{-1}

Appendix A. *Unciola inermis* production (wet weight) at Station 5-1 from July 1982 to July 1983.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
81A	Jul	51.6	8.92	0.75	11.43	589.8	-	-	-
	Nov	1.4	11.00	0.10	18.98	26.6	7.55	26.5	200.1
81B	Jul	59.8	7.45	0.42	7.26	434.1	-	-	-
	Nov	12.9	8.89	0.51	11.26	145.3	4.00	36.4	145.4
	Feb	1.7	9.62	0.20	13.62	23.2	2.36	7.3	17.2
	May	6.0	11.00	0.40	19.02	114.1	5.40	3.9	20.8
82A	Jul	11.1	5.91	0.19	4.07	45.2	-	-	-
	Nov	2.4	7.80	0.10	3.09	19.4	4.02	6.8	27.1
	Feb	18.8	7.81	0.68	3.23	154.7	0.14	10.6	1.5
	May	18.5	8.90	0.28	11.24	207.9	3.01	13.7	56.3
	Jul	32.4	9.07	0.63	11.86	384.3	0.62	25.5	15.8
82B	Jul	297.2	3.73	0.82	1.41	419.1	-	-	-
	Nov	103.7	5.38	0.75	3.34	346.4	1.93	200.5	386.9
	Feb	83.7	5.24	0.91	3.19	267.0	-0.15	93.7	- 14.1
	May	89.0	7.45	0.76	7.36	665.0	4.17	86.4	360.1
	Jul	76.2	7.61	0.40	7.65	582.9	0.29	82.6	24.0
82C?	Nov	21.0	1.77	0.31	0.22	4.6	-	-	-
83A	May	267.1	3.08	0.74	0.89	237.7	-	-	-
	Jul	65.7	6.45	0.44	5.09	334.4	4.20	166.4	698.9

Appendix A. Unciola inermis production (continued)

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $N\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
83B	May	261.1	1.50	0.17	0.14	36.6	-	-	-
	Jul	337.2	3.87	0.93	1.58	532.8	1.44	299.2	430.8

Total production:	2.37 g 0.24 m^{-2} yr^{-1}	9.88 g m^{-2} yr^{-1}
Total biomass:	5.57 g 0.24 m^{-2}	23.21 g m^{-2}
Mean biomass:	1.11 g 0.24 m^{-2}	4.64 g m^{-2}
Production/mean biomass:		2.13 yr^{-1}

Appendix A. *Unciola inermis* production (wet weight) at Station 5-28 from July 1982 to July 1983.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
81A	Jul	123.4	9.13	0.97	12.20	1505.5	-	-	-
	Nov	3.4	9.86	0.3	14.49	49.3	2.29	63.4	145.2
	Feb	2.2	10.27	0.03	16.00	22.6	1.51	2.8	3.8
	May	1.3	11.30	-	20.28	26.4	4.28	1.8	7.7
	Jul	2.0	12.25	-	24.78	49.6	4.50	1.7	7.7
81B	Jul	47.5	6.69	0.44	5.57	264.6	-	-	-
	Nov	36.5	8.30	0.48	9.49	346.4	3.92	42.0	164.6
	Feb	4.2	9.00	0.1	11.54	49.5	2.05	20.4	41.8
	May	5.2	10.06	0.25	15.22	79.1	3.68	4.7	17.3
	Jul	2.0	11.10	-	19.40	38.8	4.18	3.6	15.0
82A	Jul	72.0	5.65	0.24	3.65	262.8	-	-	-
	Nov	105.0	6.68	0.55	5.58	585.9	1.83	88.5	162.0
	Feb	51.2	6.87	0.77	6.04	309.2	0.46	78.1	35.9
	May	14.8	7.90	0.61	8.44	124.9	2.40	33.0	79.2
	Jul	28.1	8.66	0.55	10.56	296.7	2.12	21.4	45.4
82B	Jul	550.6	3.81	0.67	1.45	798.4	-	-	-
	Nov	230.8	5.00	0.82	2.82	650.9	1.37	390.7	535.3
	Feb	144.3	4.91	0.76	2.68	386.7	-0.14	187.1	- 26.3
	May	127.0	6.12	0.62	4.52	574.0	1.84	135.6	249.5
	Jul	49.2	7.16	0.65	6.64	326.7	2.12	88.1	186.8
83A	Feb	4.34	2.15	0.32	0.34	1.5	-	-	-
	May	61.6	3.02	0.58	0.82	50.5	0.48	33.0	15.8
	Jul	180.8	4.38	0.54	1.99	359.8	1.17	121.2	141.8

Appendix A. Unciola inermis production (continued)

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
83B	May	189.7	1.52	0.18	0.14	26.6	-	-	-
	Jul	38.0	3.16	0.22	0.87	33.1	0.73	113.8	83.1
83C	Jul	121.2	2.03	0.29	0.30	36.4	-	-	-

Total production:	1.91 g 0.24 m^{-2} yr^{-1}	7.97 g m^{-2} yr^{-1}
Total biomass:	7.25 g 0.24 m^{-2}	30.22 g m^{-2}
Mean biomass:	1.45 g 0.24 m^{-2}	6.05 g m^{-2}
Production/mean biomass:		1.32 yr^{-1}

Appendix A. *Ericthonius fasciatus* production (wet weight) at Station 5-1 from July 1981 to July 1982.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
F80	Jul	27.8	5.87	0.70	2.08	57.3	-	-	-
S81A	Jul	316.2	3.77	0.73	0.72	227.7	-	-	-
	Nov	7.7	7.11	0.50	3.28	25.3	2.56	162.0	414.7
S81B	Jul	471.3	2.30	0.38	0.21	99.0			
	Nov	102.9	5.36	0.54	1.64	168.8	1.43	287.1	410.6
F81A	Nov	117.8	2.59	0.66	0.30	35.3	-	-	-
	Feb	1.0	3.40	-	0.52	0.5	0.22	59.4	13.1
	May	282.3	6.05	0.82	2.25	635.2	1.73	141.6	245.0
	Jul	33.7	7.59	0.48	3.85	129.7	1.60	158.0	252.8
F81B	Nov	115.0	1.56	0.20	0.08	9.2	-	-	-
	Feb	1.0	1.60	-	0.08	0.2	-	58.5	-
	May	103.0	5.00	1.00	1.46	150.4	1.38	52.5	72.5
	Jul	69.5	5.88	0.48	2.06	143.2	0.60	86.3	51.8
S82A	May	202.2	1.42	0.15	0.06	12.1	-	-	-
	Jul	760.5	3.90	0.70	0.78	593.2	0.72	481.4	346.6
S82B	Jul	403.9	1.96	0.47	0.15	60.6	-	-	-

Total production:	1.81 g 0.24 m^{-2} yr^{-1}	7.53 g m^{-2} yr^{-1}
Total biomass:	2.35 g 0.24 m^{-2}	9.78 g m^{-2}
Mean biomass:	0.47 g 0.24 m^{-2}	1.96 g m^{-2}
Production/mean biomass:		3.84 yr^{-1}

Appendix A. *Ericthonius fasciatus* production (wet weight) at Station 5-1 from July 1982 to July 1983.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation s_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
F81A	Jul	33.7	7.59	0.48	3.85	129.7	-	-	-
F81B	Jul	69.5	5.88	0.48	2.06	143.2	-	-	-
S82A	Jul	760.5	3.90	0.70	0.78	593.2	-	-	-
S82B	Jul	403.9	1.96	0.47	0.15	60.6	-	-	-
	Nov	181.1	6.05	0.48	2.21	400.2	2.06	292.5	602.6
F82A	Nov	513.1	2.90	0.80	0.40	205.2	-	-	-
	Feb	1077.6	4.84	0.69	1.30	1400.9	0.90	795.4	715.9
	May	18.7	7.26	0.75	3.49	65.3	2.19	548.2	1200.6
	Jul	12.8	9.15	0.25	6.09	78.0	2.60	15.8	41.1
F82B	Nov	524.4	1.74	0.34	0.11	57.7	-	-	-
	Feb	612.2	3.42	0.89	0.60	367.3	0.49	568.3	278.5
	May	50.4	4.80	1.00	1.33	67.0	0.73	331.3	241.8
	Jul	149.2	7.01	0.52	3.17	473.0	1.84	99.6	183.3
S83A	Feb	436.9	1.58	0.30	0.08	35.0	-	-	-
	May	547.9	2.28	0.40	0.20	109.6	0.12	492.4	59.1
	Jul	570.8	4.65	1.06	1.24	707.8	1.04	559.4	581.8

Appendix A. Ericthonius fasciatus production (continued)

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation S_L	Mean weight $\bar{w}$(mg)	Biomass $N\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
S83B	May	439.0	1.63	0.19	0.09	39.5	-	-	-
	Jul	117.0	1.85	0.40	0.13	15.2	0.04	278.0	11.2

Total production:	3.92 g 0.24 m^{-2} yr^{-1}	16.32 g m^{-2} yr^{-1}
Total biomass:	4.45 g 0.24 m^{-2}	20.62 g m^{-2}
Mean biomass:	0.99 g 0.24 m^{-2}	4.12 g m^{-2}
Production/mean biomass:		3.96 yr^{-1}

Appendix A. *Ericthonius fasciatus* production (wet weight) at Station 5-28 from July 1982 to July 1983.

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation S_L	Mean weight $\bar{w}$(mg)	Biomass $\bar{N}\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
F81A	Jul	280.2	5.47	1.1	1.83	512.8	-	-	-
F81B	Jul	133.7	3.88	1.1	0.83	111.0	-	-	-
F82A	Jul	100.9	1.89	0.40	0.13	13.1	-	-	-
	Nov	486.1	5.87	0.96	2.21	1074.3	2.08	293.5	610.5
S82B	Jul	320.5	1.44	0.10	0.06	19.2	-	-	-
	Nov	640.2	4.94	0.55	1.35	837.3	1.29	480.4	619.7
	Feb	1.1	5.57	-	1.78	2.0	0.43	320.6	137.9
	May	30.8	7.14	0.38	3.30	101.6	1.52	15.9	24.2
	Jul	17.0	8.74	0.23	5.43	92.3	2.13	23.9	50.9
F82A	Nov	1739.8	2.53	0.60	0.28	487.1	-	-	-
	Feb	1.1	4.12	-	0.84	0.9	0.56	870.4	487.4
	May	21.8	6.06	0.39	2.21	48.2	1.37	11.4	15.6
	Jul	209.4	6.11	0.74	2.29	479.5	0.08	115.6	9.2
F82B	Nov	1436.1	1.48	0.16	0.07	100.5	-	-	-
	Feb	1.1	3.32	-	0.49	0.5	0.42	718.6	301.8
	May	84.3	3.99	0.72	0.82	69.1	0.33	42.7	12.8
	Jul	156.9	4.58	0.46	1.11	174.2	0.29	120.6	35.0
S83A	Feb	1.1	1.16	-	0.04	-	-	-	-
	May	178.7	1.40	0.11	0.06	10.7	0.02	89.9	1.8
	Jul	187.8	2.84	0.51	0.35	65.7	0.29	183.2	53.1

Appendix A. Ericthonius fasciatus production (continued)

Cohort	Month	No. in cohort N	Mean length $\bar{L}$(mm)	Standard deviation S_L	Mean weight $\bar{w}$(mg)	Biomass $N\bar{w}$(mg)	Weight increment $\Delta\bar{w}$(mg)	Mean number $\bar{N}$	Production increment $\bar{N}\Delta\bar{w}$(mg)
S83B	Jul	130.8	1.43	0.12	0.06	7.8	-	-	-

Total production:	2.36 g 0.24 m^{-2} yr^{-1}	9.83 g m^{-2} yr^{-1}
Total biomass:	4.21 g 0.24 m^{-2}	17.53 g m^{-2}
Mean biomass:	0.84 g 0.24 m^{-2}	3.51 g m^{-2}
Production/mean biomass:		2.80 yr^{-1}

APPENDIX B. Yellowtail Flounder Stomach Contents Data - Station 5

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
POLYCHAETA								
Ampharete arctica	1.55	3.11	0.08	0.27	-	-	-	-
Arabella sp. A (R)	-	-	-	-	-	-	0.05	0.72
Notomastus latericeus	-	-	0.02	0.02	0.04	0.05	-	-
Caulleriella n. sp. B	-	-	-	-	0.04	<0.01	-	-
Tharyx annulosus	-	-	-	-	0.07	0.01	-	-
Pherusa cf. falcata	-	-	0.02	0.05	-	-	-	-
Glycera capitata	-	-	-	-	-	-	0.09	0.25
Goniadella gracilis	-	-	-	-	-	-	0.09	0.03
Lumbrinerides acuta	-	-	-	-	0.04	0.03	0.42	0.21
Lumbrinerides fragilis	0.11	24.19	-	-	-	-	0.28	33.51
Clymenura polaris	0.11	0.24	0.38	2.31	0.11	0.22	0.37	1.81
Euclymene sp. A	0.23	0.20	-	< 0.01	0.14	0.08	1.48	0.72
Aglaophamus circinata	-	1.58	0.06	0.02	0.07	1.16	0.09	3.10
Ophelina acuminata	0.11	0.35	0.02	0.54	-	-	-	-
Myriochele oculata (R)	-	-	0.02	< 0.01	-	-	-	-
Aricidea catherinae	0.34	0.02	0.04	< 0.01	-	-	-	-
Aricidea cerruti	0.06	0.00	0.02	< 0.01	-	-	0.23	0.01
Phyllodoce mucosa	0.06	0.03	0.04	0.04	0.18	0.15	-	-
Polygordius sp. A	-	-	-	-	0.07	0.01	-	-
Chone duneri	0.74	0.74	0.60	1.93	0.14	0.08	0.19	0.10
Chone infundibuliformis	3.09	32.19	0.19	0.20	0.07	0.25	3.85	16.44
Megalomma bioculata (R)	-	-	0.02	0.20	-	-	-	-
Scalibregma inflatum	0.06	0.91	-	-	0.18	1.35	0.23	0.64
Pholoe minuta (R)	-	-	-	-	0.04	<0.01	-	-
Sthenelais limicola (R)	-	-	-	-	0.04	2.07	0.05	0.70
Spiophanes bombyx	-	-	-	-	0.22	0.04	0.05	-
Polydora concharum	-	-	-	-	-	0.03	-	-
Exogone hebes	-	-	-	-	-	-	0.05	<0.01
Exogone verugera	-	-	0.04	< 0.01	0.07	0.01	0.09	<0.01
Parapionosyllis longicirrata	-	-	-	-	0.04	<0.01	-	-
Polycirrus sp. D (R)	-	-	-	-	0.04	-	-	-

APPENDIX B - Station 5 (continued)

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
SIPUNCULA								
Phascolion strombi	-	-	-	-	0.04	< 0.01	0.05	0.02
GASTROPODA								
Mitrella dissimilis	-	-	-	-	0.04	0.17	-	-
BIVALVIA								
Crenella glandula	-	-	-	-	-	-	0.05	< 0.01
Arctica islandica	-	-	-	-	-	-	0.05	< 0.01
Cerastoderma pinnulatum	-	-	-	-	-	-	0.05	0.79
Enis directus (R)	-	-	-	-	0.07	0.27	-	-
CRUSTACEA								
Copepoda (P)	0.11	0.06	-	-	-	-	-	-
Cumacea								
Diastylis quadrispinosa	0.06	0.03	-	-	-	-	0.09	0.05
Diastylis sculpta	0.06	0.05	0.04	0.04	0.04	< 0.01	-	-
Lamprops quadriplicata (R)	-	-	0.02	0.01	-	-	-	-
Petalosarsia declivis	-	-	0.04	<0.01	0.07	0.01	-	-
Isopoda								
Cirolana polita	-	-	-	-	-	-	0.14	1.91
Amphipoda								
Argissa hamatipes	-	-	0.02	<0.01	0.04	<0.01	-	-
Byblis serrata	-	-	0.08	0.06	0.29	0.06	-	-
Leptocheirus pinguis	-	-	0.02	0.01	0.04	0.01	-	-
Unciola inermis	17.92	10.34	38.16	43.68	65.79	72.67	23.97	17.85
Unciola irrorata	2.40	1.47	12.43	21.19	5.76	9.56	0.74	0.67
Corophium crassicorne	-	-	0.02	< 0.01	0.33	0.12	-	-
Ericthonius fasciatus	71.38	23.51	45.00	26.42	23.57	8.80	64.63	19.46

APPENDIX B -Station 5 (continued)

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
Amphipoda (continued)								
Siphonoecetes colletti	-	-	0.04	<0.01	-	-	0.37	0.08
Hippomedon serratus	-	-	-	-	-	-	0.05	0.10
Monoculodes edwardsi (R)	-	-	0.09	0.12	-	-	-	-
Phoxocephalus holbolli	-	-	0.02	0.01	0.04	0.01	0.19	0.07
Rhepoxynius hudsoni	-	-	-	<0.01	0.07	0.04	0.09	0.04
Stenopleustes inermis	0.52	0.11	0.94	0.53	1.16	1.08	0.28	0.01
Aeginina longicornis (H)	0.74	0.59	0.94	1.06	0.54	0.79	0.60	0.27
Mysidacea								
Neomaysis americana (P)	-	-	-	0.01	-	-	-	-
Erythrops erythrophthalma (P)	-	-	-	-	-	-	0.05	0.02
Decapoda								
Pagurus spp.	0.23	0.24	0.30	0.60	0.07	0.40	-	-
Crangon septemspinosa	-	-	0.02	0.15	-	-	-	-
Natantia spp.	0.06	<0.01	0.02	0.04	-	-	-	0.08
ECHINOIDEA								
Echinarachnius parma	-	-	0.02	0.31	0.04	0.01	-	-
OPHIUROIDEA								
Amphipolis squamata	0.06	0.05	0.26	0.34	0.44	0.44	1.07	0.32
No. of stomach examined:	12		33		17		30	
No. with identifiable prey:	11		21		11		24	
No. of prey species:	22	23	35	37	38	38	32	33
Total stomach content weight (g) or numbers:	1747	6.627	5325	14.263	2762	7.730	2157	15.534
Mean fish length (cm) ± S.D.:	26.3± 5.8		32.7± 5.0		33.1± 4.1		34.3±4.0	
Mean fish weight (g) ± S.D.:	192.7±145.3		350.5±159.0		356.4±135.4		397.9±152.0	

APPENDIX B. Yellowtail Flounder Stomach Contents Data - Station 10

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
ANTHOZOA								
Cerianthus borealis (R)	-	0.02	6.95	71.03	-	-	0.81	30.30
POLYCHAETA								
Ampharete arctica (R)	4.03	0.56	-	-	-	-	0.10	0.07
Pherusa cf. falcata (R)	0.08	0.01	-	-	-	-	0.20	0.38
Glycera dibranchiata	0.23	0.51	-	-	1.14	1.42	0.10	1.00
Glycera n. sp. A	0.08	0.02	0.53	0.02	-	-	-	-
Lumbrineris fragilis	0.23	1.36	-	-	-	-	1.53	12.47
Nephtys bucera	0.23	1.24	1.07	1.71	-	-	0.10	0.17
Nereis zonata (R)	-	-	0.53	1.26	-	-	-	-
Ophelina acuminata	-	0.14	-	-	-	-	-	-
Leitoscoloplos spp. juv. (R)	-	-	-	-	-	-	0.10	0.65
Orbinia swani (R)	-	-	-	-	-	-	0.20	2.65
Paraonis pygoenigmatica	0.08	< 0.01	-	-	-	-	-	-
Polygordius sp. A	1.47	< 0.01	-	-	-	-	-	-
Chone infundibuliformis (R)	0.08	0.18	-	-	-	-	-	-
Scalibregma inflatum	0.16	0.17	-	-	1.14	0.51	-	-
Stheneiais limicola	1.09	0.59	-	-	-	-	2.03	6.11
Spiophanes bombyx	1.78	0.03	-	-	-	-	-	-
BIVALVIA								
Arctica islandica	-	-	-	-	-	-	0.10	0.14
Ensis directus (R)	-	-	1.60	0.87	-	-	-	-
Spisula solidissima	1.01	0.21	1.07	0.58	-	-	-	-
Tellina tenella	0.23	0.04	-	-	-	-	-	-

APPENDIX B - Station 10 (continued)

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
CRUSTACEA								
Copepoda (P)	4.42	0.08	-	-	-	-	0.20	0.03
Cumacea								
Pseudoleptocuma minor	1.63	0.09	-	-	-	-	1.93	0.65
Diastylis sculpta	0.08	<0.01	-	-	-	-	0.10	0.01
Lamprops quadriplicata	0.08	<0.01	-	-	-	-	-	-
Isopoda								
Cirolana polita	0.85	0.25	2.14	2.03	-	-	0.61	1.67
Amphipoda								
Byblis serrata (R)	0.16	0.03	-	-	-	-	0.20	0.04
Pseudunciola obliquua	0.16	<0.01	-	-	-	-	-	-
Unciola irrorata	0.70	0.07	-	-	-	-	0.51	0.72
Calliopius laeviusculus (P)	-	-	-	-	-	-	1.32	1.03
Ericthonius fasciatus	0.08	<0.01		-	-	-	0.20	0.02
Parahaustorius attenuatus	0.54	0.22	0.53	0.14	1.14	2.66	1.12	4.76
Protohaustroius wigleyi	1.16	0.08	1.07	0.02	-	-	0.41	0.13
Hippomedon serratus	0.08	0.01	-	-	-	-	0.10	0.21
Monoculodes edwardsi	0.23	0.01	2.14	0.02	-	-	0.71	0.25
Photis dentata (R)	-	-	0.53	0.02	-	-	-	-
Rhepoxynius hudsoni	2.25	0.15	0.53	<0.01	-	-	2.85	0.71
Dyopedos monacanthus (H)	0.16	<0.01	-	-	-	-	0.92	0.09
Pontogeneia inermis (P)	0.70	0.04	1.07	0.09	-	-	39.06	15.13
Aeginina longicornis (H)	1.71	0.12	-	-	1.14	0.14	31.43	10.78
Mysidacea								
Neomysis americana (P)	4.96	0.41	0.53	0.02	-	-	-	-

APPENDIX B - Station 10 (continued)

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
Decapoda								
Crangon septemspinosa	0.70	0.03	70.59	15.09	95.45	95.27	0.51	1.33
Dichelopandalus leptoceras (R)	0.31	0.04	-	-	-	-	-	-
Pagurus spp.	5.85	0.45	0.53	0.20	-	-	11.90	4.61
Cancer borealis (R)	4.81	0.63	-	-	-	-	-	-
Cancer irroratus (R)	-	-	2.14	1.12	-	-	0.10	0.49
Natantia spp. (R)	3.18	0.31	2.67	0.18	-	-	0.31	0.12
ECHINOIDEA								
Echinarachnius parma	1.40	2.23	3.74	5.59	-	-	0.20	3.28
UROCHORDATA								
Ascidiacea sp. C (R)	3.64	0.97	-	-	-	-	-	-
VERTEBRATA								
Brosme brosme (P)	49.07	88.71	-	-	-	-	-	-
No. of stomach examined:	244		42		9		102	
No. with identifiable prey:	176		29		6		51	
No. of prey species:	42	44	19	19	5	5	31	31
Total stomach content weight (g) or numbers:	1290	92.301	187	17.790	88	4.923	983	15.953
Mean fish length (cm) ± S.D.:	30.6±8.0		30.0±5.1		32.6±4.2		29.2±4.36	
Mean fish weight (g) ± S.D.:	322.5±222.3		273.1		338.0±134.7		246.4±117.8	

APPENDIX B. Yellowtail Flounder Stomach Contents Data - Station 13

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
POLYCHAETA								
Ampharete arctica	-	-	-	-	0.30	0.01	0.08	0.01
Anobothrus gracilis	-	-	-	-	0.12	0.10	0.24	0.04
Tharyx acutus	-	-	-	-	0.06	0.01	0.16	0.01
Tharyx annulosus	-	-	-	-	0.31	0.02	-	-
Tharyx dorsobranchialis	-	-	-	-	0.03	<0.01	0.16	<0.01
Tharyx marioni (R)	-	-	-	-	0.06	<0.01	-	-
Cossura longocirrata	-	-	-	-	0.09	<0.01	0.08	<0.01
Brada villosa	-	-	1.90	4.88	0.09	0.71	0.08	0.35
Pherusa cf. falcata	9.09	26.28	0.95	11.10	0.82	16.46	2.06	10.67
Glycera capitata (R)	-	-	-	-	0.03	<0.01	-	-
Lumbrineris fragilis	18.18	2.44	-	-		-	-	-
Lumbrineris impatiens	-	-	-	-	2.44	0.60	4.91	0.81
Lumbrineris sp. C	-	-	-	-	0.03	0.01	0.16	0.02
Ninoe nigripes	-	-	13.33	2.63	5.31	2.35	12.59	5.40
Asychis biceps	-	-	-	-	0.03	0.11	0.08	0.38
Rhodine gracilior	-	-	-	-	-	-	0.32	0.36
Aglaophamus circinata (R)	-	-	0.95	2.41	-	-	-	-
Nephtys incisa (F)		50.65	1.92	20.92	1.07	29.52	0.16	12.50
Ophelina acuminata	9.09	3.27	-	-	0.03	0.10	-	-
Aricidea catherinae	-	-	-	-	0.40	0.03	1.03	0.02
Aricidea longobranchiata	-	-	-	-	-	-		
Aricidea neosuecica (R)	-	-	-	-	0.03	<0.01		
Aricidea quadrilobata	-	-	-	-	-	-	0.08	<0.01
Aricidea suecica	-	-	0.95	0.02	0.03	<0.01	0.08	0.01
Levinsenia gracilis	-	-	-	-	3.27	0.18	3.64	0.07
Eteone longa	-	-	-	-	0.06	0.01	-	-
Eucranta villosa	-	-	-	-	-	-	0.40	0.05
Harmothoe extenuata	-	-	-	-	-	-	0.08	<0.01
Oriopsis sp. A. (R)	-	-	-	-	-	-	0.08	<0.01

APPENDIX B - Station 13 (continued)

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
POLYCHAETA (continued)								
Chone duneri	-	-	10.48	1.77	1.37	1.09	1.27	0.72
Chone infundibuliformis	27.27	9.90	21.90	43.39	4.37	29.50	23.75	57.90
Euchone incolor	-	-	-	-	0.03	<0.01	0.08	<0.01
Prionospio steenstrupi	-	-	-	-	-	-	0.08	0.01
Spio limicola	-	-	-	-	-	-	0.08	0.04
Sternaspis scutata (R)	-	-	-	-	0.03	0.87	0.08	0.24
Terebellides stroemi	-	-	-	-	0.03	0.02	0.71	0.17
BIVALVIA								
Nucula proxima	-	-	-	-	0.21	0.06	-	-
CRUSTACEA								
Copepoda (P)	-	-	-		0.03	0.01	0.16	0.01
Cumacea								
Diastylis sculpta	-	-	-	-	0.06	0.04	0.16	0.04
Eudorella pusilla	-	-	-	-	0.18	0.03	0.32	0.02
Isopoda								
Edotea triloba	-	-	0.95	0.75	-	-	0.16	0.04
Amphipoda								
Argissa hamatipes	-	-	-	-	0.18	0.04	0.32	0.04
Ampelisca agassizi	18.18	0.46	40.95	5.95	13.62	4.15	41.81	8.92
Leptocheirus pinguis	-	-	-	-	0.06	0.17	0.16	0.16
Unciola irrorata	-	-	-	-	-	-	0.24	0.12
Erichthonius fasciatus	-	-	-	-	0.15	0.04	0.32	0.05
Orchomene sp. A (R)	-	-	-	-	0.06	0.02	-	-
Casco bigelowi	9.09	6.09	-	-	0.03	0.21	0.08	0.16
Photis pollex	-	-	-	-	0.31	0.01	0.08	0.01

APPENDIX B - Station 13 (continued)

CLASS Order Species	August 1982 % numbers	 % weight	Oct., Dec. 1982 % numbers	 % weight	Feb.-March 1983 % numbers	 % weight	May 1983 % numbers	 % weight
Amphipoda (continued)								
Harpinia propinqua	-	-	-	-	0.09	0.03	0.16	0.01
Stenopleustes inermis	-	-	-	-	0.09	0.01	0.24	0.02
Dyopedos monacanthus (H)	-	-	-	-	0.03	< 0.01	0.48	0.06
Andaniopsis nordlandica (P)	-	-	-	-	-	-	0.08	0.01
Metopella angusta	-	-	-	-	0.09	0.01	0.24	0.01
Aeginina longicornis (H)	-	-	3.81	1.13	64.60	13.50	2.53	0.55
Decapoda								
Cancer borealis	9.09	0.91	1.90	5.04	-	-	-	-
No. of stomach examined:	10		26		42		27	
No. with identifiable prey:	4		9		37		21	
No. of prey species:	7	8	12	12	42	42	44	44
Total stomach content weight (g) or numbers:	11	1.313	105	1.864	3274	22.346	1263	16.469
Mean fish length (cm) ± S.D.:	33.6±4.3		30.4±3.8		33.8±3.2		32.0±2.6	
Mean fish weight (g) ± S.D.:	373.5±162.9		274.5±125.5		372.5±137.4		312.7±74.6	

(F) - fragments
(H) - lives on hydroids and bryozoans
(P) - pelagic
(R) - absent from benthic samples at this station

Appendix C. Chone infundibuliformis production (wet weight) at Station 13 from July 1982 to July 1983.

Mean number $\bar{N}(m^{-2})$	Mean length L(mm)	Mean weight w(mg)	Geometric mean wt $(w_j w_{j+1})^{0.5}$	Biomass $\bar{N}w$(mg)	Number removed $\bar{N}$	Biomass removed $\bar{N}(w_j w_{j+1})^{0.5}$
4.88	12.5	13.0	-	63.4	-	-
11.75	17.5	31.0	20.1	364.3	-6.87	-138.1
12.71	22.5	59.4	42.9	755.0	-0.96	- 41.2
8.58	27.5	99.9	77.0	857.1	4.13	318.0
1.92	32.5	154.0	124.0	295.7	6.66	825.8
-	37.5	223.1	185.4	-	1.92	355.2

Total biomass removed: 1.32 g m^{-2}
Times number of size classes: 5
Production: 6.60 g m^2 yr^{-1}
Biomass: 2.34 g m^{-2}
Production/biomass: 2.82 yr^{-1}

About the Author

Jeremy Steven Collie was born in a blizzard in Winnipeg, Manitoba, Canada, on 27 April 1958. When he was five years old his family moved to London, Ontario; in 1976 Mr. Collie graduated London Central High School. He attended one year at the University of Guelph, after which he was matriculated at the University of York, in York, England. In July 1980 Mr. Collie received a Bachelor of Science in Biology with First Class Honours from York.

In September 1980 Jeremy Collie entered the Massachusetts Institute of Technology / Woods Hole Oceanographic Institution Joint Program in Oceanography. This thesis culminates Mr. Collie's doctoral work in biological oceanography.

Mr. Collie is married to a non-oceanographer who is so cute that she prefers to remain anonymous. They live in Vancouver, British Columbia, where since September 1985 Jeremy Collie has held a position at the University of British Columbia. He pursues his research interests and those of his employer at the Institute of Animal Resource Ecology. As well, Jeremy Collie continues with his lifelong favorite activities: skiing, sailing, and other outdoor pursuits, most especially running.